THE STATUS OF PACIFIC WALRUS (*ODOBENUS ROSMARUS DIVERGENS*) FORAGING HABITAT AND DIET AROUND ST. LAWRENCE ISLAND

A

THESIS

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ABSTRACT

With ongoing climate change, food resources may be reduced for Pacific walruses (*Odobenus rosmarus divergens*). Significant differences in walrus foraging habitat (benthic communities) or diet might indicate changes in prey quality or quantity. In this study, benthic infaunal biomass, abundance, and composition were compared between 1970-1974 and 2006 at stations southwest of St. Lawrence Island. Sediment grain size was compared because it strongly determines benthic community structure. Wet weights, counts, and species composition of prey items found in stomachs of walruses collected near the island were compared between the 1980s and 2007. Benthic invertebrate biomass and abundance increased mainly due to high Nuculidae biomass and abundance, although results may be skewed by low sample size. Silt fractions increased regionally. No significant dietary differences were detected in walruses. Walruses may have undergone a population redistribution or decline in response to benthic community changes that would be undetected in stomach content analyses.

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GENERAL INTRODUCTION

Benthic communities are extremely variable and patchily distributed because of many physical and biological interactions. For example, substrate type greatly influences the distribution of benthic marine invertebrates because many have specific requirements and/or preferences for sediment grain size and/or chemical composition due to variations in feeding styles and habitat (e.g., epifaunal vs. infaunal) (Stoker 1978, Sirenko and Koltun 1992). Currents can influence variation in the amount and composition of sediments, food (carbon), and nutrients deposited to the benthos (Grebmeier and Cooper 1995, Grebmeier and Dunton 2000). Fluxes in larval settlement and mortality (produced by natural causes, predation, disturbances, and/or competition) can dictate colonization of available habitat (Raimondi 1991, Gaines and Bertness 1993, Gosselin and Qian 1997, Wahl 2001). Additionally, alterations in sea water temperature can modify fecundity and predation rates among marine organisms (Pechenik 1984, Hoegh-Guldberg and Pearse 1995, Nomaguchi et al. 1997, Napp et al. 2000, Hunt et al. 2002).

Within the Bering Sea, benthic communities are greatly influenced by sea ice extent and duration because late sea ice retreat, associated with earlier phytoplankton blooms, allows great quantities of food (i.e. carbon production) to reach the benthos (Sambrotto et al. 1986, Stabeno et al. 1998, Grebmeier and Dunton 2000, Eslinger and Iverson 2001, Stabeno et al. 2001). High primary production reaches the benthos during early blooms due to cold water temperatures restricting zooplankton grazing (Napp et al. 2000, Hunt et al. 2002). Distributions of Bering Sea benthic communities are subsequently influenced by the transport and deposition of carbon by water mass

formation and hydrographic flow (Grebmeier and Dunton 2000). The highest benthic biomass regions occur southwest of St. Lawrence Island, in the central Gulf of Anadyr, and in the Chirikov Basin (Grebmeier and Dunton 2000, Grebmeier et al. 2006). Benthic faunal biomass declines north of a biomass hotspot in the southern Chukchi Sea (Grebmeier et al. 2006). Benthic communities south of St. Lawrence Island tend to be dominated by bivalves, amphipods, and polychaetes (Grebmeier 1993, Grebmeier and Cooper 1995, Grebmeier et al. 1995). The area north of St. Lawrence Island to Bering Strait is dominated by amphipods and bivalves (Feder et al. 1994, Grebmeier and Dunton 2000).

During winter/early spring, a wind-driven ice-free area develops along the southern coast of St. Lawrence Island. The annual formation of the St. Lawrence Island Polynya (SLIP) maintains an area of cold water, a "cold pool," (Coachman et al. 1975), associated with high productivity and nutrients (Grebmeier and Cooper 1995). Additionally, brine injection during sea ice formation within the SLIP creates currents that transport and entrain organic matter to the southwest of St. Lawrence Island (Pease 1980, Overland and Pease 1982) resulting in this region having extremely high benthic invertebrate biomass (Grebmeier and Cooper 1995).

Over the last 20+ years, annual ice extent and thickness have declined in the Bering Sea (Maslanik et al. 1996, Vinnikov et al. 1999, Parkinson 2000, Comiso 2002, Parkinson and Cavalieri 2002, Comiso 2003, Serreze et al. 2005, Serreze et al. 2007). Reductions in winter ice cover and higher air temperatures have subsequently caused a reduction in the summertime extent of the SLIP cold pool (Wyllie-Echeverria and

Wooster 1998). Increased settling of fine-grained sediments has been reported in the SLIP region possibly due to alterations in circulation (Grebmeier and Cooper 1995). These changes, as well as other climate-related processes, may be contributing to changes and declines in bivalve and amphipod biomass within and north of the SLIP (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995, Grebmeier et al. 1995, Grebmeier and Dunton 2000, Moore et al. 2003, Grebmeier and Cooper 2004, Dunton et al. 2005, Grebmeier et al. 2006).

Declines in bivalve and amphipod biomass within and north of the SLIP over the last 20+ years may have a large impact on the health and survival of walruses, bearded seals, gray whales, and spectacled eiders because they all selectively forage in these areas for one or both of these prey types (Fay et al. 1977, Feder and Jewett 1981, Grebmeier and Harrison 1992, Highsmith and Coyle 1992, Petersen et al. 1998). For example, gray whales primarily consume dense patches of ampeliscid amphipods in the Chirikov Basin and spectacled eiders selectively forage for the bivalve *Nuculana pernula* (Lovvorn et al. 2003, Moore et al. 2003).

Pacific walruses (*Odobenus rosmarus divergens*) may be particularly vulnerable to declines or changes in bivalve populations since decreasing summer sea ice may lead to overexploitation of food resources near coastlines and remaining ice by walruses (Pungowiyi 2000, Marz 2006). Walruses forage within the SLIP as they travel between wintering areas in the central Bering Sea and summering grounds either in the Chukchi Sea (females and calves) or in the southeastern and western Bering Sea (males) (Fay 1982). Walruses are extremely important to Yupik communities on St. Lawrence Island

who depend on migrating walruses for meat, ivory, and hides (Langdon 1995, Garlich-Miller and Burn 1999). Concern exists that reduced summer sea ice in the Bering Sea has decreased food availability for walruses as increasingly larger numbers compete for food near terrestrial haulouts or in restricted areas of the remaining sea ice (Pungowiyi 2000, Marz 2006). Presently, the health and size of the Pacific walrus population is unknown, although a population estimate is underway (Dr. Suzann G. Speckman, USGS, pers. comm.). However, indications exist that walruses may have approached the carrying capacity of the system such as lower reproductive rates in female walruses in the 1990s (Garlich-Miller et al. 2006). Emaciated female walruses and abandoned calves were reported along the Beaufort Sea coast in the summers of 2002, 2004, and 2007 (Metcalf and Robards 2008). Additionally, unusual walrus migratory and behavioral patterns were observed by Native hunters in recent years (Metcalf and Robards 2008).

It is possible that either top-down (if walruses have exceeded their carrying capacity) or bottom-up (changes in sediment, circulation, carbon supply, etc.) processes are reducing food resources for walruses. Ultimately, the carrying capacity for predators is related to preferred prey availability and to changes in foraging habitat structure (Hunt et al. 2002). Therefore, this thesis addressed whether significant differences have occurred within the SLIP over the last 20+ years in benthic community biomass and community structure, and in walrus diet. In Chapter 1, infaunal invertebrate biomass, abundance, and composition within a SLIP study area were compared between 1970-1974 and 2006 stations to look for evidence of significant changes in benthic community structure between years. The proportion of benthic stations classified as silt (based on

sediment modal phi size) was also compared between years within the study area to evaluate if differences in benthic community composition could be associated with differences in sediment grain size. Hypotheses tested were that between stations sampled in 1970-1974 and stations sampled in 2006 1) invertebrate biomass and abundance were not significantly different, (2) invertebrate community structure was not significantly different, and (3) sediment composition was not significantly different.

In Chapter 2, wet weights, counts, and species composition of prey items found in stomachs of walruses were compared between samples collected in 1980s and 2007 to evaluate if significant changes in diet have occurred in walruses foraging near St. Lawrence Island. For this, one-gallon stomach samples were collected by subsistence hunters on St. Lawrence Island. Hypotheses tested include that between the 1980s and 2007 (1) the frequency of occurrence of prey items in walrus stomachs was not significantly different, (2) prey counts in walrus stomachs were not significantly different, and (3) prey weights were not significantly different.

LITERATURE CITED

Coachman LK, Aagaard K, Tripp RB (1975) Bering Strait: the regional physical oceanography. University of Washington Press, Seattle, WA

Comiso JC (2002) Correlation and trend studies of the sea-ice cover and surface temperatures in the Arctic. Ann Glaciol 34:420-428

Comiso JC (2003) Warming trends in the Arctic from clear-sky satellite observations. J Clim 16:3498-3510

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic–pelagic coupling in the western Arctic: role of cross-shelf advective processes. Deep-Sea Res II 52:3462-3477

Eslinger DL, Iverson RL (2001) The effects of convective and wind-driven mixing on spring phytoplankton dynamics in the southeastern Bering Sea middle shelf domain. Cont Shelf Res 21:627-650

Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N Am Fauna 74:1-279

Fay FH, Feder HM, Stoker SW (1977) An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. National Technical Information Service, Report PB-273-505, Springfield, VA

Feder HM, Jewett SC (1981) Feeding interactions in the eastern Bering Sea with emphasis on the benthos. In: Hood DW, Calder J (eds) The eastern Bering Sea shelf: oceanography and resources, Vol II, University of Washington Press, Seattle, pp 1229-1261

Feder HM, Naidu AS, Jewett SC, Hameedi JM, Johnson WR, Whitledge TE (1994) The northeastern Chukchi Sea: benthos-environmental interactions. Mar Ecol Prog Ser 111:171-190

Gaines SD, Bertness M (1993) The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology 74:2430-2435

Garlich-Miller JL, Burn DM (1999) Estimating the harvest of Pacific walrus, *Odobenus rosmarus divergens*, in Alaska. Fish Bull 97:1043-1046

Garlich-Miller JL, Quakenbush LT, Bromaghin JF (2006) Trends in age structure and productivity of Pacific walruses harvested in the Bering Strait Region of Alaska, 1952-2002. Mar Mamm Sci 22:880-896

Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates. Mar Ecol Prog Ser 146:265-282

Grebmeier JM (1992) Benthic processes on the shallow continental shelf. In: Nagel P (ed) Results of the third joint US-USSR Bering & Chukchi Sea expedition (BERPAC), summer 1988, U.S. Fish and Wildlife Service, Washington DC, pp 243-251

Grebmeier JM (1993) Studies on pelagic-benthic coupling extended onto the Russian continental shelf in the Bering and Chukchi Seas. Cont Shelf Res 13:653-668

Grebmeier JM, Cooper LW (1995) Influence of the St. Lawrence Island Polynya on the Bering Sea benthos. J Geophys Res 100:4439-4460

Grebmeier JM, Cooper LW (2004) Biological implications of Arctic change, Oral Session 2: Paper 2. In: The ACIA international symposium on climate change in the Arctic: extended abstracts. AMAP Report 2004:4, Reykjavik, Iceland, pp 1-4

Grebmeier JM, Dunton KH (2000) Benthic processes in the northern Bering/Chukchi Seas: status and global change. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Marine Mammal Commission Workshop, Girdwood, AK, pp 80-93

Grebmeier JM, Harrison NM (1992) Seabird feeding on benthic amphipods facilitated by gray whale activity in the northern Bering Sea. Mar Ecol Prog Ser 80:125-133

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt L (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Grebmeier JM, Smith WO, Conover RJ (1995) Biological processes on Arctic continental shelves, ice-ocean-biotic interactions. In: Smith WO, Grebmeier JM (eds) Arctic oceanography: marginal ice zones and continental shelves: Coastal Estuarine Stud 49:231-261

Highsmith RC, Coyle KO (1992) Productivity of Arctic amphipods relative to gray whale energy requirements. Mar Ecol Prog Ser 83:141-150

Hoegh-Guldberg O, Pearse JS (1995) Temperature, food availability, and the development of marine invertebrate larvae. Am Zool 35:415-425

Hunt Jr. GL, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res II 49:5821-5853

Langdon SJ (1995) Increments, ranges, and thresholds: human population responses to climate change in northern Alaska. In: Peterson DL, Johnson DR (eds) Human ecology and climate change: people and resources in the far north. Taylor & Francis, Washington DC, pp 139-152

Lovvorn JR, Richman SE, Grebmeier JM (2003) Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. Polar Biol 26:259-267

Marz S (2006) Ice-dependent marine mammals in Alaska: a survey of background information and issues of concern regarding: ice Seals, Pacific walrus, polar bears and bowhead whales. Alaska Oceans Program Report, Anchorage, AK

Maslanik JA, Serreze MC, Barry RG (1996) Recent decreases in Arctic summer ice cover and linkages to atmospheric circulation anomalies. Geophys Res Lett 23:1677-1680

Metcalf V, Robards M (2008) Sustaining a healthy human-walrus relationship in a dynamic environment: challenges for comanagement. Ecol Appl 18 (Supplement):S148 - S156

Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Can J Zool 81:734-742

Napp JM, Kendall Jr. AW, Schumacher JD (2000) A synthesis of biological and physical processes affecting the feeding environment of larval walleye Pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fish Oceanogr 9:147-162

Nomaguchi TA, Nishijima C, Minowa S, Hashimoto M, Haraguchi C, Amemiya S, Fujisawa H (1997) Embryonic thermosensitivity of the ascidian, *Ciona savignyi*. Zool Sci 14:511-516

Overland JE, Pease CH (1982) Cyclone climatology of the Bering Sea and its relation to sea ice extent. Mon Wea Rev 110:5-13

Parkinson CL (2000) Variability of Arctic sea ice: the view from space, an 18-year record. Arctic 53:341-358

Parkinson CL, Cavalieri DJ (2002) A 21 year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. Ann Glaciol 34:441-446

Pease CH (1980) Eastern Bering Sea ice processes. Mon Wea Rev 108:2015-2023

Pechenik JA (1984) The relationship between temperature, growth rate, and duration of planktonic life for larvae of the gastropod *Crepidula fornicata* (L). J Exp Mar Biol Ecol 74:241-257

Petersen MR, Piatt JF, Trust KA (1998) Foods of spectacled eiders *Somateria fischeri* in the Bering Sea, Alaska. Wildfowl 49:124-128

Pungowiyi C (2000) Native observations of change in the marine environment of the Bering Strait region. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Marine Mammal Commission Workshop, Girdwood, AK, pp 26-29

Raimondi PT (1991) Settlement behavior of *Chthamalus anisopoma* larvae largely determines the adult distribution. Oecologia 85:349-360

Sambrotto RN, Niebauer HJ, Goering JJ, Iverson RL (1986) Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Cont Shelf Res 5:161-198

Serreze MC, Barrett A, Lo F (2005) Northern high latitude precipitation as depicted by atmospheric reanalyses and satellite retrievals. Mon Wea Rev 113:3407-3430

Serreze, MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533-1536

Sirenko BI, Koltun VM (1992) Characteristics of benthic biocenoses of the Chukchi and Bering Seas. In: Nagel P (ed) Results of the third joint US-USSR Bering and Chukchi Seas expedition (BERPAC), summer 1988. U.S. Fish and Wildlife Service, Washington DC, pp 251-261

Stabeno PJ, Bond NA, Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the southeastern Bering Sea. Fish Oceanogr 10:81-98

Stabeno PJ, Schumacher JD, Davis RF, Napp JM (1998) Under-ice observations of water column temperature, salinity, and spring phytoplankton dynamics: eastern Bering Sea shelf. J Mar Res 56:239-255

Stoker S (1978) Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. PhD Thesis, University of Alaska Fairbanks, AK

Vinnikov KV, Robock A, Stouffer RJ, Walsh JE, Parkinson CL, Cavalieri DJ, Mitchell JFB, Garrett D, Zakharov VF (1999) Global warming and northern hemisphere ice extent. Science 286:1934-1937

Wahl W (2001) Small scale variability of benthic assemblages: biogenic neighborhood effects. J Exp Mar Biol Ecol 258:101-114

Wyllie-Echeverria T, Wooster WS (1998) Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish Oceanogr 7:159-170

CHAPTER 1:

A temporal comparison of benthic community structure southwest of St. Lawrence Island between 2006 and 1970-1974[1]

1.1 ABSTRACT

Invertebrate biomass and abundance may be changing in Bering Sea benthic infaunal communities. This study compared benthic invertebrate biomass, abundance, and infaunal community composition between 1970-1974 and 2006 at stations in an area southwest of St. Lawrence Island. Invertebrate biomass and abundance were significantly greater in 2006 than in 1970-1974 primarily due to high nuculid (Bivalvia) biomass and abundance that contributed 13.15 % (biomass) and 8.54 % (abundance) to differences in community structure. Nuculids may have increased between 1970-1974 and 2006 due to enhanced settling of silt within the overall St. Lawrence Island Polynya region since the late 1980s. Results suggest that bivalve biomass and abundance may be higher, or be more patchily distributed, than previously thought. Patchiness in bivalve biomass and abundance, spatial scale, selective predation, a strong recruitment event and/or sampling design may account for the differences between this study and previous studies.

1.2 INTRODUCTION

Polynyas are recurring ice-free areas in arctic seas (Cooper et al. 2002). The St. Lawrence Island Polynya (SLIP) forms each winter south of St. Lawrence Island (SLI) in the Bering Sea (Cooper et al. 2002). As cold, salty water is created from brine injection

[1] Merrill T (2008) A temporal comparison of benthic community structure southwest of St. Lawrence Island between 2006 and 1970-1974. Prepared for submission in *Polar Biology*.

during sea ice formation within the SLIP, ocean currents are altered so that water and organic matter are transported to the southwest of SLI (Stabeno and Reed 1994, Grebmeier and Cooper 1995, Schumacher and Stabeno 1998). By forming in the same area annually, the SLIP maintains an area of cold water (a cold pool) associated with nutrient-rich conditions and high productivity due to the entrainment of organic matter (Nihoul et al.1993, Grebmeier and Cooper 1995). High productivity from phytoplankton blooms subsequently reaches the seafloor in the spring, supporting benthic food webs (Napp et al. 2000, Hunt et al. 2002). Therefore, the SLIP is an important foraging ground for benthic-feeding mammals and sea birds, such as walruses, gray whales, and spectacled eiders (Grebmeier and Cooper 1995).

Over the last 20+ years, extent and thickness of both annual and multiyear sea ice have declined as a result of climate change (Maslanik et al. 1996, Vinnikov et al. 1999, Parkinson 2000, Comiso 2002, Parkinson and Cavalieri 2002, Comiso 2003, Serreze et al. 2005, Serreze et al. 2007). Lower winter ice cover and higher air temperatures have caused a contraction of the summertime extent of the SLIP cold pool (Wyllie-Echeverria and Wooster 1998). Concern exists as to the effect this, along with other climate-related processes, will have on predators and food availability in the Bering Sea (Grebmeier et al. 2006). Declines in several marine mammals and sea birds in the Bering Sea, such as northern fur seals, kittiwakes, and murres have been linked to reductions in key prey species since the 1970s (Hunt et al. 2002). Since the 1990s, there have been reported declines and/or northerly shifts in foraging grounds of bottom-feeding birds and mammals in the Bering Sea such as spectacled eiders and gray whales (Stehn et al. 1993,

Lovvorn et al. 2003, Moore et al. 2003, Moore et al. 2006). Within the SLIP and north of SLI, benthic infaunal invertebrate biomass has been reported to be in decline since the mid-1980s (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995, Grebmeier et al. 1995, Grebmeier and Dunton 2000, Moore et al. 2003, Grebmeier and Cooper 2004, Dunton et al. 2005, Grebmeier et al. 2006, Coyle et al. 2007). For example, declines in biomass and changes in bivalve community (taxonomic) composition have been observed since 1988 (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004). Previous benthic studies (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004) examined large scale trends in benthic infaunal invertebrate biomass, abundance, and community composition but smaller, local/regional trends may be different and can be relevant to benthic predator populations that have limited foraging ranges (Menge et al. 1997).

Benthic communities throughout the SLIP were sampled in 1970-1974 and distinguished through cluster analysis (Stoker 1978). One community type was distributed southwest of St. Lawrence Island and was dominated by selective detritus-feeding bivalves, such as *Macoma calcarea* (Tellinidae) and *Eunucula bellotii* (Nuculidae), and the filter feeding ascidian, *Pelonaia corrugata* (Stoker 1978). This benthic community was originally classified based on 11 stations as a "sub-group" of a larger cluster group (Benthic Cluster Group VIII, Subgroup A-1 in Stoker 1978, Figures 1.1, 1.2). Stations within this community were re-sampled in 1984 and 1990 (Grebmeier 1987, Grebmeier and Cooper 1995).

Declines in infaunal invertebrate biomass and abundance among benthic communities within the SLIP since the mid-1980s may result in reduced prey quality or quantity for bottom-feeding predators such as spectacled eiders and walruses. Biomass, abundance, and community composition of benthic infauna were assessed in 2006 at stations that were located within the boundaries of Benthic Cluster Group VIII, Subgroup A-1 (in Stoker 1978) to evaluate the current status of this SLIP community.

Substrate type is a physical factor that can greatly influence benthic community structure (assemblages) since marine invertebrates differ in their feeding types, habitat (epifaunal vs. infaunal), preferences for certain sediment grain size and/or chemical composition (Stoker 1978, Sirenko and Koltun 1992). Within the SLIP region, recent observations suggest increased settling of fine-grain sediments (clays), possibly due to changes in circulation patterns brought about by climate change (Dr. Jacqueline Grebmeier, University of Maryland, Center for Environmental Science, pers. comm.).

Three major water masses (Bering Shelf Water, Alaska Coastal Water and Bering Shelf/Anadyr Water) regulate local hydrography in the Bering Sea (Figure 1.1) and hence, influence sediment grain size (Fleming and Heggarty 1966, Coachman et al. 1975, Coachman 1993, Stabeno et al. 1999). Within the central Bering Sea, cold, salty Bering Shelf water (temperature (t) = 1-2°C and salinity (s) = 32.4 to 32.7‰) flows past St. Lawrence Island on the west and east sides. Along the Alaska coast, warm Alaska coastal water (t = up to 10°C and s = 31.5 to 32.1‰) dominates (Coachman 1987). Flow along the Alaskan coast of the northern Bering Sea is a combination of river runoff (mainly the Yukon River) and a continuation of the Bering Coastal Current (BCC)

(Stabeno et al.1999). The BCC consists of waters from the Gulf of Alaska's Alaska Coastal Current (ACC) that flows through the Aleutian Chain (Schumacher and Stabeno 1998). Anadyr water (t = -0.5 to 2°C and s = 32.8 to 33.1‰) originates along the Bering Sea continental slope and flows eastward as a continuation of the Bering Slope Current (BSC) across the shelf along the southern coast of the Chukotka Peninsula (Grebmeier 1987, Overland and Roach 1987). In the Gulf of Anadyr, a major gyre of Anadyr water exists that originates at depth over the slope and outer continental shelf (Coachman and Shigaev 1992). North of St. Lawrence Island, Anadyr and Bering shelf water mix, combining characteristics of both as Bering shelf/Anadyr (BS/A) water. Ultimately, Bering shelf/Anadyr and Alaska coastal water masses exit the Bering Sea through Bering Strait into the Chukchi Sea (Coachman et al. 1975). It is speculated that a decrease over the last 20+ years in the intensity of the Gulf of Anadyr Gyre and/or in the northward transport of water through Bering Strait has been driving changes in SLIP benthic communities through increased settling of fine-grained sediments (Grebmeier and Cooper 1995, Grebmeier and Dunton 2000). Interestingly, reduced water flow was reported through Bering Strait in the 1990s and between 1998 and 2001 (Roach et al. 1995, Woodgate et al. 2006).

This study addressed multiple hypotheses pertaining to the benthic infaunal community southwest of St. Lawrence Island (Benthic Cluster Group VIII, Subgroup A-1 in Stoker 1978). Specifically, I hypothesized that between stations sampled in 1970-1974 and stations sampled in 2006 1) invertebrate biomass and abundance were not

significantly different, (2) invertebrate community structure was not significantly different, and (3) sediment composition was not significantly different.

1.3 METHODS

In March 2006, seven stations were sampled opportunistically during a three week cruise aboard the Russian ice-breaker, *Magadan*, which visited walrus foraging areas south of St. Lawrence Island (Figure 1.2). Water depth and GPS coordinates were recorded at each station (Appendix 1.1). As time allowed, five benthic faunal samples and one sediment sample were taken at each station using a 0.1 m^2 van Veen grab. Five benthic faunal samples were taken per station to reduce variability and replicate the protocol used in the 1970-1974 study (Stoker 1978) to which the 2006 data were compared. Benthic faunal samples were sieved through a 1 mm screen onboard the ship. All animals retained on the screen were preserved in 10% buffered formalin for later sorting and analysis at the University of Alaska Fairbanks. Faunal samples were transferred into 50% isopropanol.

To determine if infaunal invertebrate biomass, abundance, and community composition were different between stations sampled in 1970-1974 and 2006, all faunal samples were re-sieved using a 2.8 mm sieve (Stoker 1978 used a 3 mm sieve), and sorted to family, blotted dry, weighed to the nearest centigram, and counted. Intact organisms and fragments of organisms with distinctive head regions were counted to determine abundance. If fragments of headless organisms could be identified to family, they were included in the wet weights. Unidentified fragments were classified into broader taxonomic categories, such as polychaete or bivalve fragments, weighed and

assigned a total count of one. Wet weights for mollusks included shells. All counts and weights were multiplied by 10 (since the sampling area of the vanVeen Grab is 0.1 m^2) to obtain biomass in wet weight (grams/m^2) and abundance in individuals/m^2. Fragments or diagnostic hard parts of organisms lacking tissue were not included in counts or weights. Dominant invertebrates were those which had the largest wet weights and/or abundances among samples.

After square-root transformation, mean invertebrate biomass and abundance were compared between 1970-1974 (sieved using 3 mm mesh) and 2006 (sieved using 2.8 mm mesh) stations that fell spatially within the same sampling area (Table 1.1, Figure 1.2, Benthic Cluster Group VIII, Subgroup A-1 in Stoker 1978) through Analysis of Variance (ANOVA). Coefficients of variation were calculated for 1970-1974 and 2006 average biomass values to assess spatial variability among stations sampled in the two time periods. Similarities in community composition, based on square-root transformed abundance and biomass data, were compared between stations sampled in those years using several multivariate analyses such as one-way ANOSIM (Analysis of Similarity), SIMPER (Similarity Percentages Routine) and MDS (Multi-dimensional Scaling) plots. All multivariate analyses were performed using the statistical software package *Primer-E* v6.

To determine if significant differences existed in wet weight (grams), abundance and/or community composition of invertebrates between 1 mm and 2.8 mm sieve fractions, three samples from each station sampled in 2006 (with the exceptions of stations 1 and 6) were sorted and analyzed prior to being sieved through a 2.8 mm screen.

One mm sieve fractions from station 1 were not sorted or analyzed because data from station 1 were not initially anticipated to be included in analyses as it fell spatially outside the study area. At station 6, only two 1 mm sieve fractions were collected due to time constraints. Animals retained on the screens were sorted to family, blotted dry, weighed, and counted. Mean invertebrate biomass and abundance data, after being square-root transformed, were compared between sieve fractions (1 mm and 2.8 mm) through Analysis of Variance (ANOVA). Similarities in community composition, based on square-root transformed abundance and biomass data, were compared between sieve fractions using multivariate analyses (one-way ANOSIM, SIMPER and MDS plots).

Although limited, 1984 (n = 1) and 1990 benthic faunal data (n = 23) were compared to 1970-1974 and 2006 data to explore temporal trends (Table 1.1). Data from 1984 and 1990 were combined because only one station sampled in 1984 fell within the study area. Using 1 mm sieve fractions, square-root transformed mean biomass data were compared with a t-test between 1984/1990 and 2006 stations that fell spatially within Benthic Cluster Group VIII, Subgroup A-1. Mean biomass was also compared between 1970-1974 and 1984/1990 stations using a t-test although 1970-1974 data were from 3 mm sieve fractions and data from 1984/1990 were from 1 mm sieve fractions (Table 1.1). Stoker (1978) showed that biomass does not significantly differ between 1 mm and 3 mm sieve fractions. Abundance data could not be compared between 1970-1974 and 1984/1990 stations because abundance can vary significantly between 1 mm and 3 mm sieve fractions (Stoker 1978).

Sediment mode grain size was determined according to the standard protocol

established by Folk and Ward (1957) for all 2006 stations except station 3. Approximately 10-15 g of each sample was placed in a beaker and dried overnight in an oven between 75-80° C, then weighed on an electronic balance to the nearest centigram. Each dry sample was then mixed in a blender for about two minutes with enough distilled water to completely cover the blender's blade (approximately 100 ml) and then sieved through 0.0625 mm mesh over a china dish to separate fine fraction mud (< 63 micron size) and coarse fraction (≥ 63 micron). The mud fractions were poured into 1000 ml graduated cylinders and suspensions were brought up to 1 liter by adding distilled water. To disperse aggregated particles into single discrete grains, two grams of sodium hexametaphosphate salt were added to each suspension and homogenized using a stirrer. The coarse fractions retained on the 0.0625 mm sieve were washed into beakers and dried in an oven at 75-80° C for 24 hours. Course fraction total weights were recorded to the nearest centigram using an electronic balance. The dry, coarse fractions were then dry sieved through nested screens (stacked upon each other). Nested sieves had 4 mm, 2 mm, 0.25 mm, 0.125 mm and 0.0625 mm respectively screens. Material retained on each sieve (top to bottom) was weighed using the electronic balance to the nearest centigram. From these fine-fraction suspensions, time-series (20 sec, 1 min 45 sec, 4 min 43 sec, 28 min, 1 hr 51 min, 7 hr 4 min, 14 hr 44 min) 25-ml samples (using a 25 ml pipette) were taken at selected depths (20, 20, 15, 10, 10, 10, 5 cm respectively) of the fine fraction suspensions. These 25-ml samples were placed into pre-weighed beakers and dried in an oven at 75-80° C for 24 hours. Dry weights were determined using a Mettler balance to the nearest milligram.

The proportion of sampled stations classified as silt, based on sediment mode phi sizes, was compared between 1970-1974 (Stoker 1978) and 2006 within Benthic Cluster Group VIII, Subgroup A-1 (in Stoker 1978) using a z-test. This was done to determine if sediment composition was significantly different between stations sampled in 1970-1974 and in 2006 (Table 1.1). To evaluate if increased settling of fine-grained sediments may be occurring throughout the SLIP, the proportion of stations classified as silt were compared between 1970-1974 and 1990 throughout the entire polynya using a z-test (Figure 1.3, Table 1.1).

1.4 RESULTS

Based on 3 mm sieve fractions, mean infaunal biomass (grams per m^2) and abundance (individuals per m^2) were significantly lower (ANOVA, $F = 201.54$, $df = 1$, $p \leq 0.0001$) for stations sampled in 1970-1974 ($n = 9$) relative to stations sampled in 2006 ($n = 7$) within Benthic Cluster Group VIII, Subgroup A-1 (in Stoker 1978). Average wet weight ± standard error (SE) was 170.13 ± 36.95 grams per m^2 for stations sampled in 1970-1974 and was 520.84 ± 97.56 grams per m^2 for stations sampled in 2006. In 1970-1974, average wet weight ± SE per station ranged from 6.79 ± 2.41 to 362.03 ± 65.74 grams per m^2 (Figure 1.4, Appendix 1.2). In 2006, average wet weight ± SE per station ranged from 193.0 ± 49.21 to 960.46 ± 24.62 grams per m^2 (Figure 1.4, Appendix 1.2). Based upon Coefficients of Variation, standard deviation was 65% of mean biomass in 1970-1974 and 50% in 2006. Average abundance ± SE was significantly lower (ANOVA, $F = 359.01$, $df = 1$, $p \leq 0.0001$) for stations sampled in 1970-1974 (625 ± 148 individuals per m^2) compared to stations sampled in 2006 (1699 ± 272 individuals per

m^2). In 1970-1974, average abundance ± SE per station ranged from 116 ± 15 to 1558 ± 251 individuals per m^2 (Appendix 1.2). In 2006, average abundance ± SE per station ranged from 874 ± 94 to 2583 ± 130 individuals per m^2 (Appendix 1.2).

Benthic community (taxonomic) composition between 1970-1974 and 2006 was moderately, but significantly, different based on biomass (Figure 1.5, ANOSIM, Global $R = 0.368$, $p = 0.002$) but highly significantly different based on abundance (Figure 1.6, ANOSIM, Global $R = 0.657$, $p = 0.001$). Station 1 was included in these analyses, as well as in all others, because it was not found to be significantly different in community composition from other 2006 stations based upon multi-dimensional scaling (MDS) plots. Within the study area, infaunal invertebrate abundance (individuals/m^2) was dominated by the families Pontoporeiidae, Nuculanidae, and Tellinidae in 1970-1974 (Table 1.2). Families Nuculanidae and Tellinidae also dominated wet weight (grams/m^2) (Table 1.2). In 2006, bivalve families (Nuculidae, Tellinidae and Nuculanidae) dominated biomass while polychaete families (Orbiniidae, Maldanidae, Cirratulidae, Capitellidae, and Glyceridae) and Nuculidae dominated abundance (Table 1.2).

SIMPER analyses revealed that differences in Nuculidae biomass and abundance contributed the most to differences in community structure between 1970-1974 and 2006 stations (Tables 1.3 and 1.4). For all SIMPER analyses, the top ten families contributing to differences in community structure between groups were listed in tables since these families accounted for at least 2/3 of the average dissimilarity. Average Nuculidae wet weight ± SE was 8.88 ± 2.89 grams per m^2 for stations sampled in 1970-1974 and was 183.07 ± 51.25 grams per m^2 for stations sampled in 2006, contributing 13.15% towards

observed differences (Table 1.3). Average Nuculidae abundance ± SE was 32 ± 9 individuals per m^2 for stations sampled in 1970-1974 and was 419 ± 143 individuals per m^2 for stations sampled in 2006, contributing 8.54% towards observed differences (Table 1.4). Although faunal families were analyzed in this study, *Eunucula bellotii* was the major species of the family Nuculidae.

Average wet weight ± SE did not differ significantly between 1 mm (n = 6) and 2.8 mm (n = 6) sieve fractions in 2006 (ANOVA, $F = 0.031$, $df = 1$, $p = 0.862$). Average wet weight ± SE was 589.23 ± 95.13 grams per m^2 for 1 mm sieve fractions and was 581.97 ± 92.53 grams per m^2 for 2.8 mm sieve fractions in 2006. However, average abundance ± SE was significantly different between sieve fractions. Average abundance ± SE was 3829 ± 289 individuals per m^2 for 1 mm sieve fractions and was 1878 ± 269 individuals per m^2 for 2.8 sieve fractions (ANOVA, $F = 249.12$, $df = 1$, $p \leq 0.0001$). Community composition (taxonomic assemblages) based on biomass was not significantly different between 1 mm (n =6) and 2.8 mm (n = 6) sieve fractions (Figure 1.7, ANOSIM, $R = -0.098$, $p = 0.775$). However, community composition based on abundance was little to moderately, but significantly, different between sieve fractions (Figure 1.8, ANOSIM, $R = 0.341$, $p = 0.009$). Although percentage contribution values were similar among families, SIMPER analysis revealed that differences in the abundance of the polychaete family Orbiniidae contributed the most to differences observed between sieve fractions (Table 1.5). Average abundance ± SE of Orbiniidae was 429 ± 154 individuals per m^2 for 1 mm sieve fractions and was 256 ± 86 individuals per m^2 for 2.8 mm sieve fractions, contributing 5.73% to the difference. There were also

decreases in small individuals among bivalve families (Table 1.5). The total number of identifiable invertebrate families in 1 mm sieve fractions was 51 compared to 39 in 2.8 mm sieve fractions (Appendix 1.3).

When biomass was compared between 3 mm sieve fraction data from stations sampled in 1970-1974 (n = 9) and 1 mm sieve fraction data from stations sampled in 1984/1990 (n = 8), mean biomass ± SE was not significantly different (t = -1.81, p = 0.1079). Mean biomass ± SE was 170.13 ± 36.95 grams per m^2 for stations sampled in 1970-1974 and was 385.92 ± 113 grams per m^2 for stations sampled in 1984/1990. Based on 1 mm sieve fractions, mean biomass was not statistically different (t = -1.37, p = 0.1946) between 1984/1990 (n = 8) stations and 2006 stations (n = 6). Mean biomass ± SE was 589.23 ± 95.13 grams per m^2 for stations sampled in 2006. Mean abundance ± SE was significantly different (t = -4.52, p = 0.0007) between 1984/1990 stations (2000 ± 283 individuals per m^2) and 2006 stations (3829 ± 289 individuals per m^2).

The majority of sediment samples in 1970-1974 (44.4%, n = 9) were very fine sand while stations sampled in 2006 (50%, n = 6) were predominately silt within the study area (Figure 1.9). However, no significant differences were detected between 1970-1974 (n = 9) and 2006 in the proportion of stations classified as silt (z = -1.67, p = 0.0952). Average modal phi sizes ± SE were 3.92 ± 0.42 in 1970-1974 and 5.33 ± 0.76 in 2006. Average modal phi sizes could not be compared between years because of bimodal distributions. A significantly lower proportion of stations were classified as silt in 1970-1974 (10.5%, n = 38) compared to 1990 (43.5%, n = 23) within the entire SLIP region (z = -2.97, p = 0.0030).

1.5 DISCUSSION

Contrary to other Bering Sea studies conducted in the 1990s and in 2001 (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004), the results of this study suggest a possible increase in benthic infaunal biomass and abundance between 1970-1974 and 2006, primarily due to high biomass and abundance of the bivalve family Nuculidae. *Eunucula bellotii* was the major bivalve present in this family (pers. obs.). The findings of this study are intriguing because studies conducted in the 1990s indicated declines in *E. bellotii* and *Macoma calcarea* (Tellinidae) within the SLIP (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004) compared to the mid-80s (Stoker 1981, Feder et al. 1985). In contrast, *Nuculana pernula* (Nuculanidae) had increased within the SLIP and expanded westerly into the Gulf of Anadyr (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004).

Several explanations are possible for the observed high values in 2006. The area sampled could have experienced a strong recruitment event of *Eunucula bellotii* in recent years. *Eunucula bellotii* has a short, pelagic larval stage with larvae dispersing and settling from August through September (Fetzer and Arntz 2008). Alternatively, *E. bellotii* biomass (and that of the whole infaunal community) may actually have steadily increased over time in this particular area while it decreased on a larger scale sampled in the above-cited studies. Since the findings of this study indicated possible increases in benthic biomass and abundance between 1984/1990 and 2006 (rather than only between

1970-1974 and 2006), higher Nuculidae biomass and abundance among 2006 stations compared to 1970-1974 stations may reflect an actual temporal trend rather than a single recruitment event.

Effects of selective predation on other species in the study area may account for potential increases in Nuculidae. The 2006 sampling occurred at stations where bivalve biomass and predation pressure from walruses, spectacled eiders, gastropods and other predators were high (Fay and Stoker 1982a, Fay and Stoker 1982b, Fay et al. 1989, Lovvorn et al. 2003). For example, a high percentage of empty *Nuculana pernula* shells in 2006 had holes in them (pers. obs.), which is characteristic of gastropod predation (Hart and Palmer 1987, Grey et al. 2005, Morton et al. 2007). Spectacled eiders (*Somateria fischeri*) selectively consume *N. pernula* in the Bering Sea (Lovvorn et al. 2003). Despite higher energy content per gram in *Eunucula bellotii*, spectacled eiders appear to prefer *N. pernula* over *E. bellotii* (of the same length classes) possibly because of the increased expenditure of energy needed to crush the thick shell of *E. bellotii* (Lovvorn et al. 2003). If *N. pernula* is being selectively consumed by predators within the study area, then *E. bellotii* may be impacted less by predation pressure and so establish dominance. For instance, spectacled eiders prefer bivalves within the size range of 18-30 mm and *E. bellotii* tends to be smaller than these lengths (Lovvorn et al. 2003).

Sampling strategy also may have influenced the results of this study. In 2006, benthic sampling occurred opportunistically at a few locations within a small area. In the post-1980 studies used for comparison to this study, sampling encompassed a larger geographic area and included a greater number of stations within the SLIP (Grebmeier

1987, Grebmeier and Cooper 1995). Therefore, spatial scale may account for the observed differences between the findings of this and previous studies. Local biotic processes, such as competition and predation, tend to dominate community assembly and organization and can vary widely among benthic communities (Huston 1999). The effects of local biotic processes, though, are obscured at larger scales, such as regionally, because environmental heterogeneity is aggregated (Huston 1999). Identifying local trends is important since predator populations may be affected by local changes in prey base (Johnson and Sherry 2001, Oro and Furness 2002).

It is possible that the high biomass and abundance of Nuculidae observed in this study is specific to the local benthic community. However, high abundance of *Eunucula bellotii* also was occasionally observed in patches outside the area sampled in this study, but within the SLIP in 2006 (Dr. Jacqueline M. Grebmeier, University of Maryland, Center for Environmental Science, pers. comm.). Patchy distribution of benthic marine invertebrates, particularly bivalves, is common (Stoker 1978, Feder et al. 1980, Grebmeier 1987, Grebmeier and Cooper 1995). Patchiness can be caused by variable substrate conditions, predation, and/or larval dispersal (Stoker 1978). It is possible, therefore, that Nuculidae and Tellinidae abundance may be actually higher within the SLIP than previously thought. Since 2006 stations were not at the exact locations of the 1970-1974 stations, it also is possible that spatial variability influenced the results. 2006 stations had a fairly high Coefficient of Variation of biomass.

Grebmeier and Cooper (1995) theorized that declines in *Macoma calcarea* and the subsequent expansion of *Nuculana pernula* into the Gulf of Anadyr is being driven

by increased settling of fine-grained sediments within the SLIP. *Nuculana pernula* may be better adapted than *M. calcarea* for muddier sediments (where oxygen may be deficient) because of monofunctional gills (more efficient respiration) and an ability to utilize the energy released from sulfur bacteria (Sirenko and Koltun 1992). Polychaete families, Orbiniidae, Maldanidae, Pectinariidae, Terebellidae, and Ampharetidae appear to prefer sand and/or mud habitats since they are deposit feeders (Holthe 1986, Kirkegaard 1992, Kirkegaard 1996). Although no significant differences were found within the study area between 1970-1974 and 2006 in the proportion of stations classified as silt, the proportion of stations classified as silt may have increased regionally (within the entire SLIP region) between 1970-1974 and 1990 (Figure 1.3, Grebmeier and Cooper 1995). Therefore, increased settling of fine-grained sediments within the SLIP may be supported despite the non-significant difference within the study area. It is possible that differences were not detected between 1970-1974 and 2006 stations because of small sample sizes.

Enhanced deposition of silt southwest of St. Lawrence Island may be related to changes in the circulation patterns and/or influx rates of the Yukon or Kuskokwim Rivers because these rivers are sources of terrigenous sediments (clays) in this area (Naidu and Mowatt 1983, Dr. Tom Weingartner, University of Alaska Fairbanks, pers. comm.). For example, as a result of climate change, increased rainfall, glacial and/or snow melt could all potentially increase Yukon River discharge into the Bering Sea during summer months (Brabets et al. 2000). Reduced and/or delayed sea ice formation in the Bering Sea may enable stronger waves to be produced during fall and winter storms with greater

open distances in which to travel. Therefore, more fine-grain sediments may be re-suspended and ultimately deposited southwest of St. Lawrence Island due to enhanced wave activity (Dr. Tom Weingartner, University of Alaska Fairbanks, pers. comm.). Storm-generated wave heights along the entire west coast of North America have increased significantly during the past three decades (Komar et al. 2000). Large inter-annual summer variation exists in the extent of inner domain water on the Alaska continental shelf, which can extend into the southwest region of St. Lawrence Island (Takenouti and Ohtani 1974). Over the last 20+ years, an expanded or more westerly summertime boundary of inner domain coastal water may increase the deposition of silt southwest of St. Lawrence Island (Dr. Kenneth Coyle, University of Alaska Fairbanks, pers. comm.).

Although significantly higher benthic biomass and abundance in this study were contrary to other findings, results of the sieve fraction comparison were in agreement with a previous study (Stoker 1978). The sizes of mesh screens used to sieve benthic infaunal samples have varied among studies. Mesh sizes have ranged from 0.5 mm to 3 mm (Stoker 1978, Feder et al. 1980, Grebmeier 1987, Sirenko and Koltun 1992, Grebmeier and Cooper 1995). This study's finding agree with Stoker (1978) who found that invertebrate abundance significantly varied between 1 mm and 3 mm (2.8 mm in this study) sieve fractions although biomass did not since the majority of biomass is included within 3 mm sieve fractions. Examining invertebrate abundance in benthic communities, in addition to biomass, is important because the dominance of organisms that do not have much mass can be underestimated by biomass (Stoker 1978). The implications for future

benthic studies are that 1 mm sieve fractions may take longer to sort than 2.8 mm sieve fractions since they contain more fauna. However, 1 mm sieve fractions may provide additional information since these retain numbers of small bivalves and polychaetes.

In conclusion, significantly higher benthic infaunal biomass and abundance were found at stations sampled in 2006 versus stations sampled in 1970-1974 within a specific area of the SLIP. The differences were largely due to the high abundance and biomass of the bivalve family Nuculidae in the 2006 samples. Nuculidae were reported to have declined within the SLIP since the mid-1980s (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004). Although data were limited in the study area (and hence a temporal trend between the 1970s and 2006 could not be determined), these results suggest that community type-specific, local sampling might yield different results than large-scale regional sampling regarding temporal changes in the Bering Sea benthic communities. The merit of each sampling strategy is dependent upon the scope of the scientific question being addressed. Detecting localized changes in the prey base of bottom-feeding predators in the Bering Sea may be critical to understanding how these predators are being impacted by changing food resources. Therefore, community type-specific, local sampling designs should be utilized in addition to larger, regional sampling designs in future studies examining Bering Sea benthic communities.

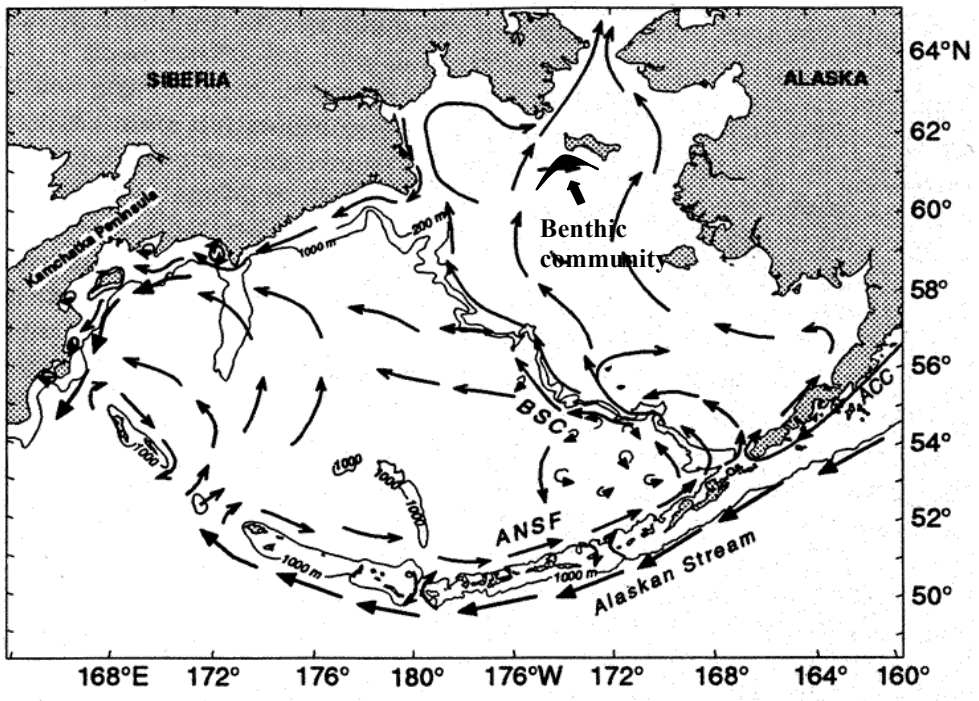

Figure 1.1. Schematic diagram of circulation in the upper 40 m of the water column in the Bering Sea (after Stabeno and Reed 1994, Schumacher and Stabeno 1998). The Alaskan Stream, Alaska Coastal Current (ACC), Bering Slope Current (BSC), and Aleutian North Slope Flow (ANSF) are indicated. Approximate location of sampled benthic community (Benthic Cluster Group VIII, Subgroup A-1) is shown.

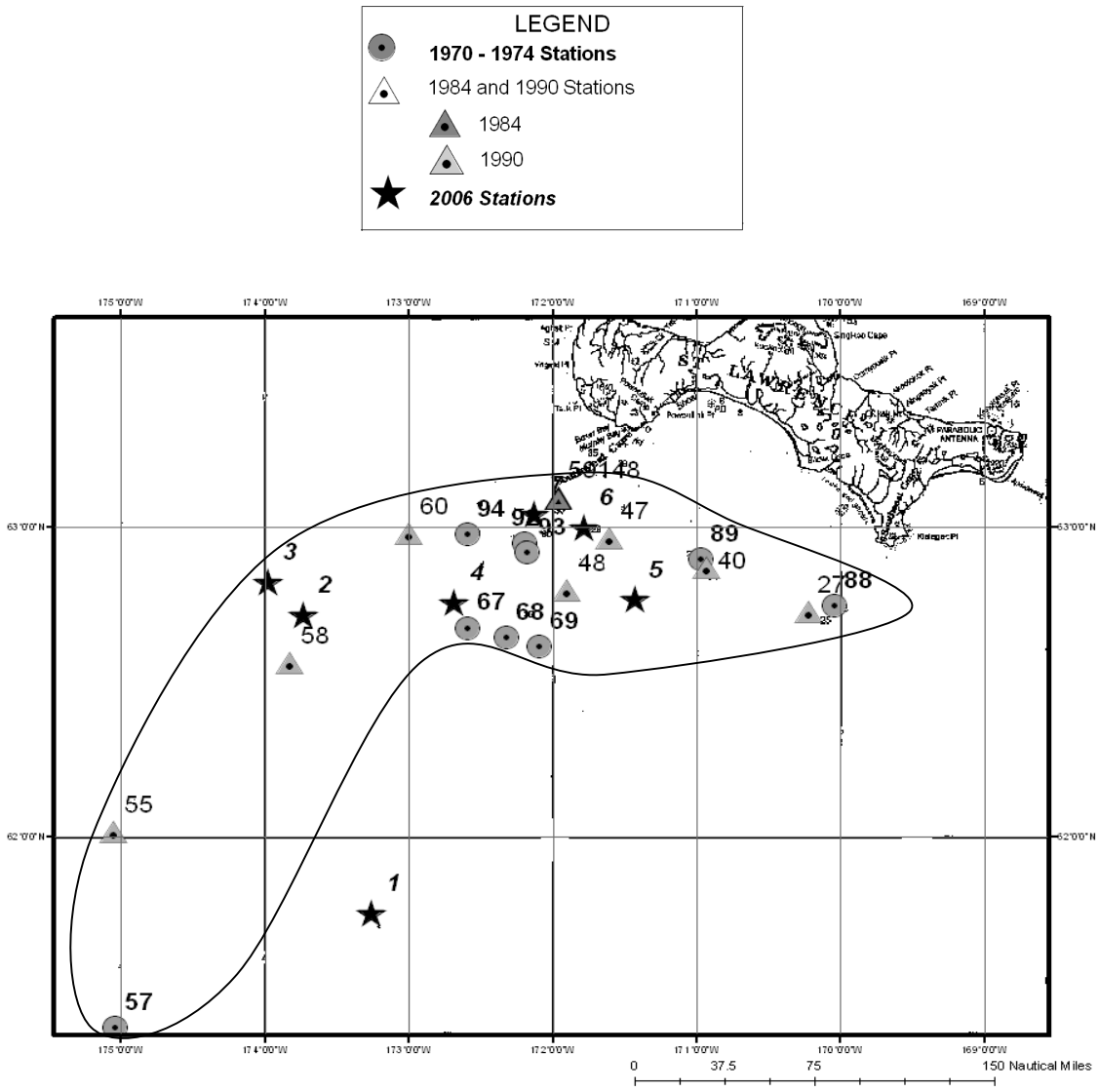

Figure 1.2. Stations sampled (by year) from which benthic data were compared. Bold font = 1970-1974 station numbers. Bold and italicized font = 2006 station numbers and non-bold font = 1984 and 1990 station numbers). Boundary of Benthic Cluster Group VIII, Subgroup A-1(in Stoker 1978) is shown.

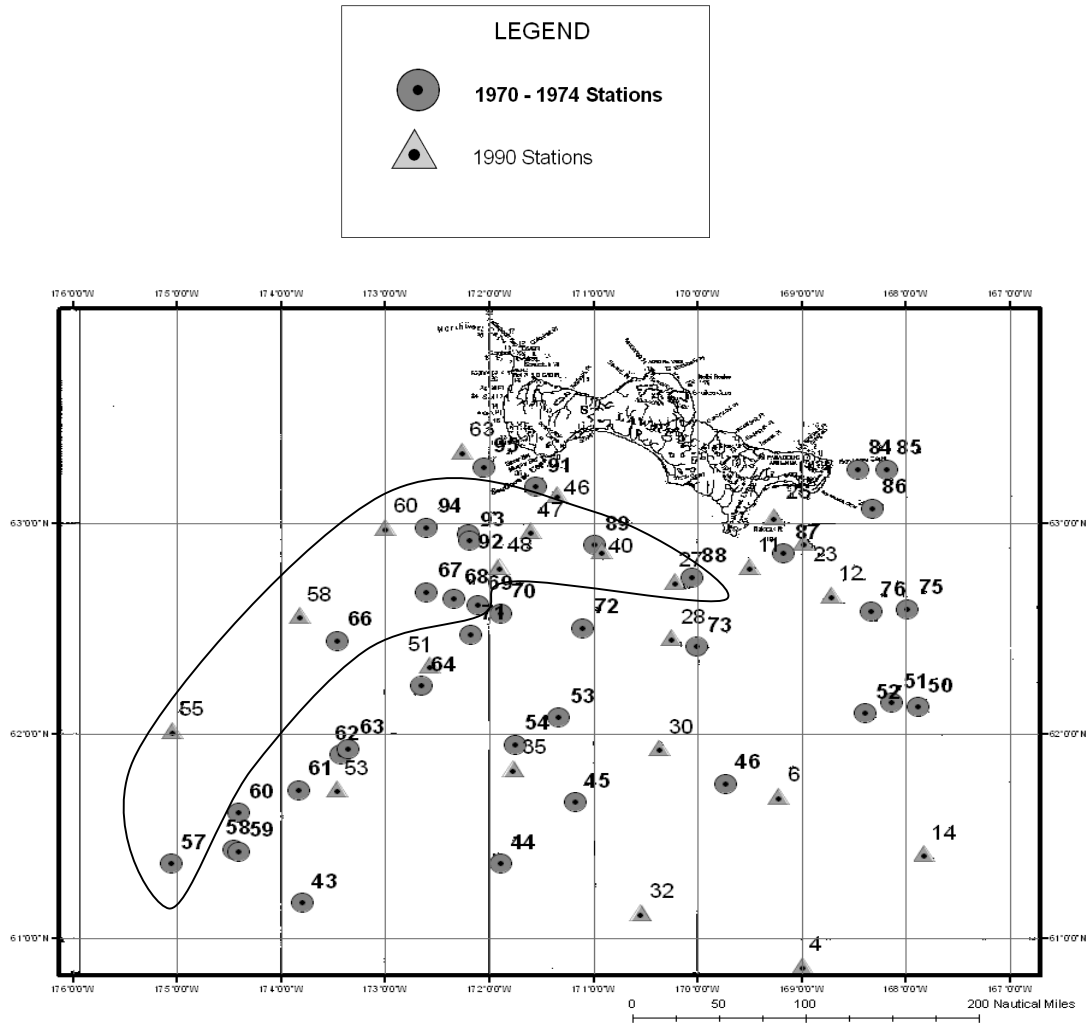

Figure 1.3. Stations within the St. Lawrence Island Polynya where sediment samples were collected in 1970-1974 and 1990. Bold font = 1970-1974 station numbers and non-bold font = 1990 station numbers). Boundary of Benthic Cluster Group VIII, Subgroup A-1(in Stoker 1978) is shown.

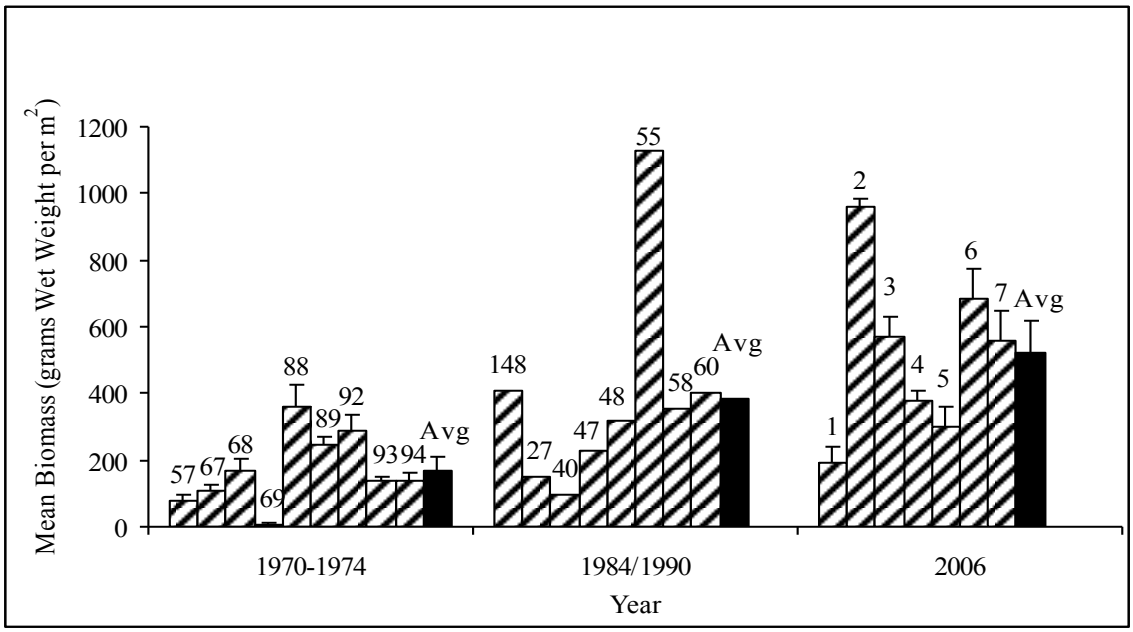

Figure 1.4. Average wet weight (grams) ± 1 standard error per station by year. Station numbers appear above bars. Average wet weight (grams) ± 1 standard error by year (1970-1974, 1984/1990 and 2006) is represented in black. Standard deviations (used to calculate standard errors) were unavailable for all stations sampled in 1984/1990.

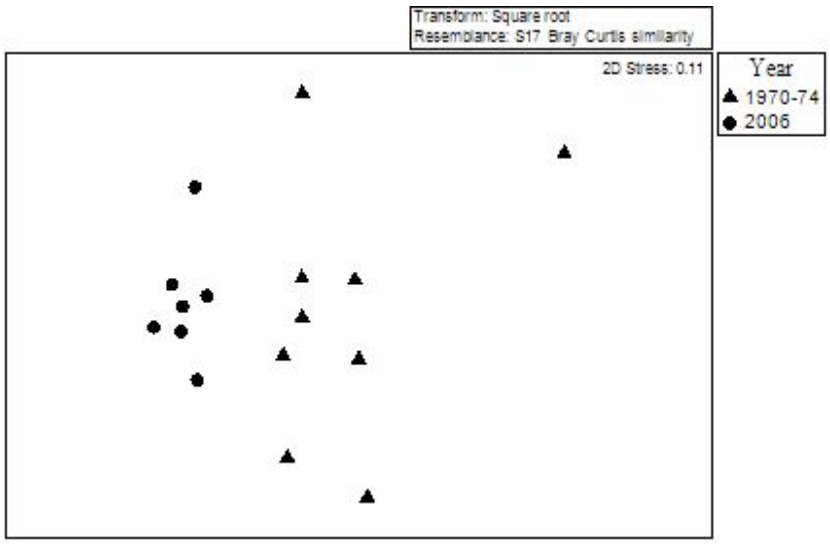

Figure 1.5. MDS plot showing the similarity of infaunal communities at stations in the St. Lawrence Island Polynya sampled in 1970-1974 (n = 9) and 2006 (n = 7) based on square-root transformed biomass data (2.8 mm mesh).

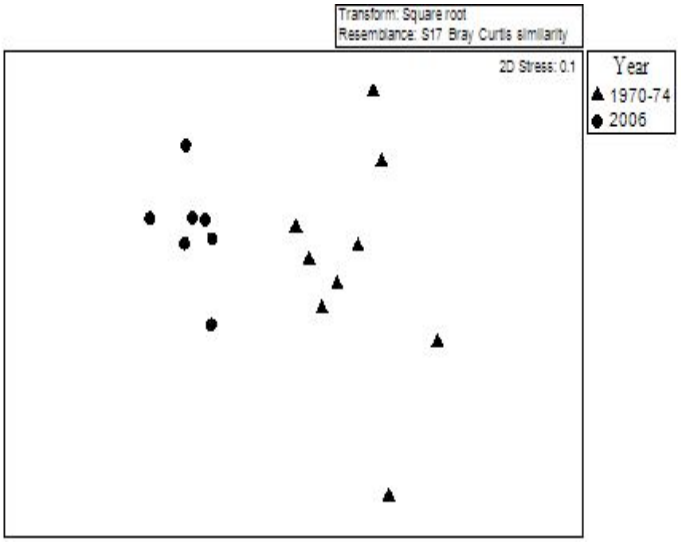

Figure 1.6. MDS plot showing the similarity of infaunal communities at stations in the St. Lawrence Island Polynya sampled in 1970-1974 (n = 9) and 2006 (n = 7) based on square-root transformed abundance data (2.8 mm mesh).

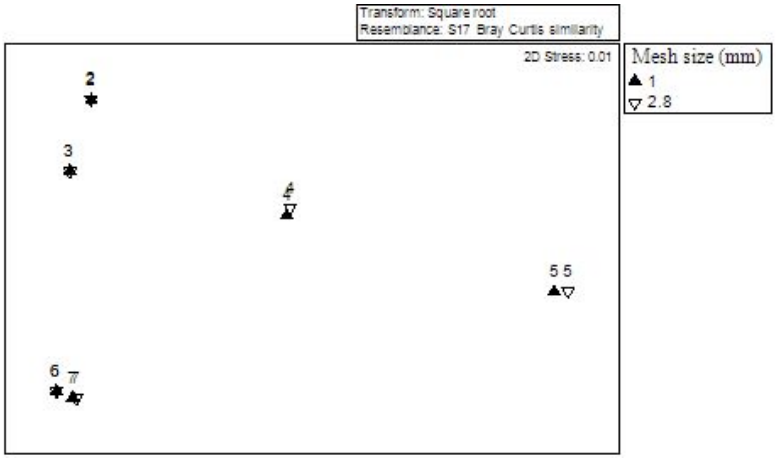

Figure 1.7. MDS plot showing the similarity of infaunal communities at stations in the St. Lawrence Island Polynya sampled in 2006 (n = 7) by sieve fractions (1 or 2.8 mm) based on square-root transformed biomass data. Numbers represent station numbers.

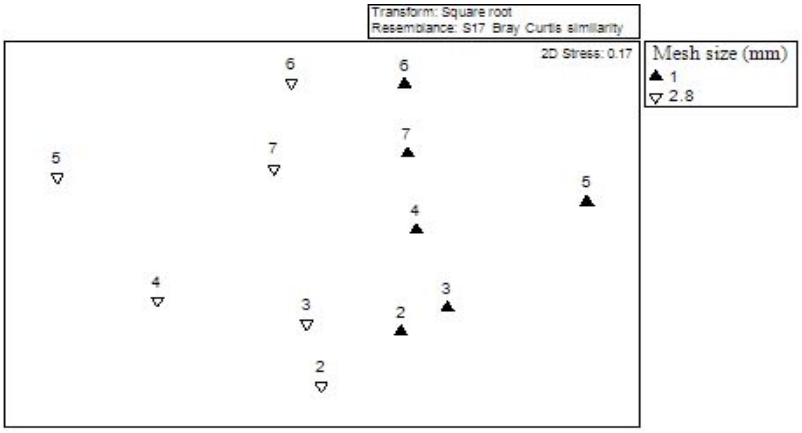

Figure 1.8. MDS plot showing the similarity of infaunal communities at stations in the St. Lawrence Island Polynya sampled in 2006 (n = 7) by sieve fractions (1 or 2.8 mm) based on square-root transformed abundance data. Numbers represent station numbers.

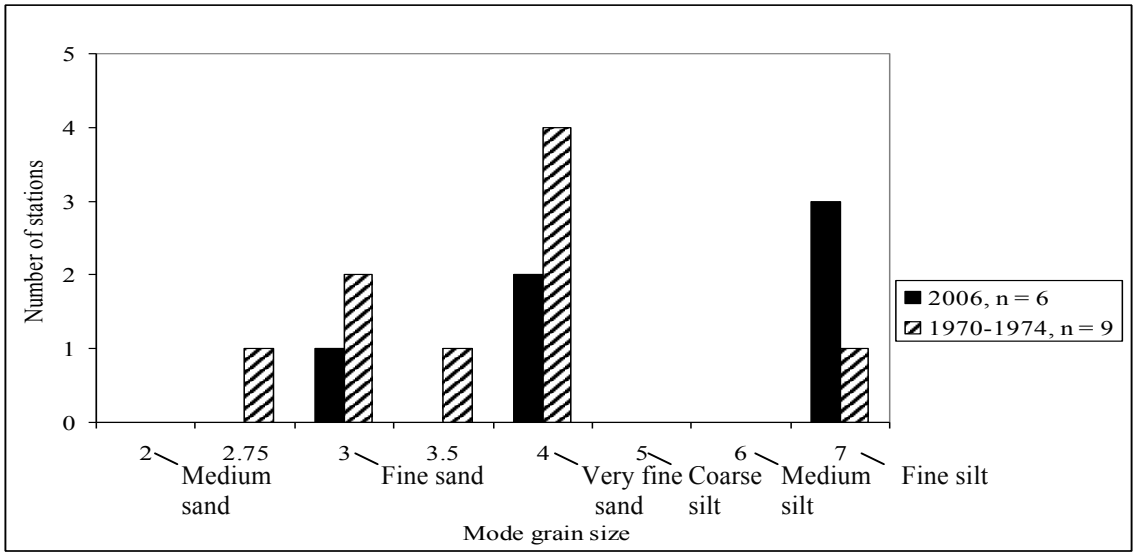

Figure 1.9. Number of stations in the St. Lawrence Island Polynya sampled in 1970-1974 (n = 9) and 2006 (n = 6) by sediment modal phi size.

Table 1.1. Summary and description of benthic data compared between stations sampled in 1970-1974, 1984/1990, and 2006 within the St. Lawrence Island Polynya. * = 3 mm sieve fraction data used in comparison. X = indicates data compared between sampled stations.

Description of data compared	1970-1974 stations	1984/1990 stations	2006 stations
3 mm benthic biomass and abundance data compared within study area	X n = 9		X n = 7
1 mm benthic biomass data compared within study area	X* n = 9	X n = 8	X n = 6
1 mm benthic abundance data compared within study area		X n = 8	X n = 6
Sediment data compared within study area	X n = 9		X n = 6
Sediment data compared within St. Lawrence Island Polynya	X n = 38	X n = 23	

Table 1.2. Biomass and abundance of the dominant infaunal benthic families (≥ 10% of total values) at each station sampled in 1970-1974 and 2006. Order of station numbers between years is not correlated to locations. Actual percents in parentheses.

1970-1974 Station number	Dominant families/ taxonomic groups by biomass	Dominant families/ taxonomic groups by Abundance	2006 Station Number	Dominant families/ taxonomic groups by biomass	Dominant families/ taxonomic groups by abundance
57	Nuculanidae (73%) Nuculidae (12%)	Pontoporeiidae (28%) Nuculanidae (26%) Nuculidae (17%)	1	Tellinidae (28%) Mytilidae (26%)	Maldanidae (15%) Capitellidae (15%) Ampeliscidae (14%)
67	Mytilidae (18%) Nuculanidae (15%) Styelidae (14%)	Pontoporeiidae (48%) Nuculanidae (11%)	2	Nuculidae (46%) Nuculanidae (26%) Tellinidae (11%)	Nuculidae (46%) Nuculanidae (12%) Tellinidae (10%)
68	Ophiuridae (17%) Styelidae (16%) Naticidae (13%)	Pontoporeiidae (21%) Nuculidae (20%) Tellinidae (18%)	3	Nuculidae (41%) Tellinidae (22%)	Nuculidae (20%) Orbiniidae (16%) Tellinidae (11%)
69	Rhynocoela (31%) Pontoporeiidae (11%)	Pontoporeiidae (21%) Tellinidae (13%) Nuculanidae (13%)	4	Nuculidae (39%) Nuculanidae (21%) Tellinidae (14%)	Nuculidae (30%) Nuculanidae (10%)
88	Veneridae (26%) Styeldiae (20%) Anthozoa (11%)	Pontoporeiidae (25%) Ampeliscidae (23%) Isaeidae (17%)	5	Nuculidae (48%) Cardiidae (20%)	Nuculidae (48%) Tellinidae (15%) Glyceridae (12%)

Table 1.2. Cont'd. Biomass and abundance of the dominant infaunal benthic families (≥ 10% of total values) at each station sampled in 1970-1974 and 2006. Order of station numbers between years is not correlated to locations. Actual percents in parenthesis.

1970-1974 Station number	Dominant families/ taxonomic groups by biomass	Dominant families/ taxonomic groups by Abundance	2006 Station Number	Dominant families/ taxonomic groups by biomass	Dominant families/ taxonomic groups by abundance
89	Cardiidae (16%) Gastropoda (12%)	Pontoporeiidae (21%) MyrioTrochidae (15%)	6	Nuculidae (28%) Ophiuridae (18%) Tellinidae (17%)	Orbiniidae (21%) Cirratulidae (14%) Nuculidae (12%)
92	Styelidae (25%) Tellinidae (18%) Ophiuridae (12%)	Pontoporeiidae (34%) Amphictenidae (27%)	7	Tellinidae (36%) Nuculidae (21%) Ophiuridae (20%)	Orbiniidae (22%) Nuculidae (11%) Tellinidae (10%)
93	Tellinidae (22%) Styelidae (20%) Ophiuridae (19%)	Pontoporeiidae (18%) Tellinidae (11%) Orbiniidae (11%)			
94	Ophiuridae (29%) Nuculanidae (18%)	Pontoporeiidae (24%) Ophiuridae (15%) Nuculanidae (12%)			

Table 1.3. Top ten families contributing to the differences observed in benthic infaunal community composition in the St. Lawrence Island Polynya between 1970-1974 (n = 9) and 2006 (n = 7) based on SIMPER analysis of square-root transformed biomass.

Family	Group 1970-74 Av.Bio (grams/m^2)	Group 2006 Av.Bio (grams/m^2)	Contrib%
Nuculidae	8.88	183.07	13.15
Tellinidae	15.07	97.57	8.20
Ophiuridae	17.50	61.14	6.19
Nuculanidae	13.28	56.37	5.54
Amphictenidae	14.65	34.84	5.49
Styelidae	26.04	0.00	4.71
Maldanidae	0.05	9.52	3.79
Naticidae	3.44	11.20	3.26
Mytilidae	2.42	12.59	3.02
Cardiidae	7.17	8.65	2.69

Table 1.4. Top ten families contributing to the differences observed in benthic infaunal community composition in the St. Lawrence Island Polynya between 1970-1974 (n = 9) and 2006 (n = 7) based on SIMPER analysis of square-root transformed abundance.

Family	Group 1970-74 Av.Abund (numbers/m^2)	Group 2006 Av.Abund (numbers/m^2)	Contrib%
Nuculidae	32	419	8.54
Orbiniidae	32	215	4.92
Maldanidae	1	71	4.77
Pontoporeiidae	176	59	4.36
Amphictenidae	37	100	4.36
Cirratulidae	1	92	4.25
Capitellidae	0	45	3.51
Tellinidae	60	151	3.37
Glyceridae	0	44	3.14
Ophiuridae	26	60	2.96

Table 1.5. Top ten families contributing to the differences observed in benthic infaunal community composition in the St. Lawrence Island Polynya among 2006 benthic sieve fractions (1 mm and 2.8 mm) based upon SIMPER analysis of square-root transformed abundance.

Family	Group 1 Av. Abund (numbers/m^2)	Group 2.8 Av. Abund (numbers/m^2)	Contrib%
Orbiniidae	429	256	5.73
Nuculanidae	359	102	5.54
Nuculidae	784	521	5.23
Cirratulidae	265	108	4.95
Tellinidae	433	174	4.49
Leuconidae	187	26	4.18
Thyasiridae	79	3	3.94
Glyceridae	92	55	3.59
Pontoporeiidae	97	48	3.47
Chiridotidae	74	61	3.43

1.6 LITERATURE CITED

Brabets TP, Wang B, Meade RH (2000) Environmental and hydrologic overview of the Yukon River Basin, Alaska and Canada. U.S. Geological Survey, Report 99-4204, Anchorage, AK

Coachman LK (1987) Advection and mixing on the Bering-Chukchi Shelves. In: ISHTAR 1986 Progress Report, Vol I, Component A. Advection and mixing of coastal water on shelf of the north Bering/Chukchi Shelves. IMS, University of Alaska Fairbanks, AK pp 211-255

Coachman LK (1993) On the flow field in the Chirikov Basin. Cont Shelf Res 13:481-508

Coachman LK, Aagaard K, Tripp RB (1975) Bering Strait: the regional physical oceanography, University of Washington Press, Seattle, WA

Coachman LK, Shigaev VV (1992) Northern Bering-Chukchi Sea ecosystem: the physical basis. In: Nagel, PA (eds) Results of the third joint US-USSR Bering and Chukchi Seas expedition (BERPAC), summer 1988. U.S. Fish and Wildlife Service, Washington DC, pp 388-398

Comiso JC (2002) Correlation and trend studies of the sea-ice cover and surface temperatures in the Arctic. Ann Glaciol 34:420-428

Comiso JC (2003) Warming trends in the Arctic from clear-sky satellite observations. J Clim 16:3498-3510

Cooper LW, Grebmeier JM, Larsen IL, Egorov VG, Theodorakis C, Kelly HP, Lovvorn JR (2002) Seasonal variation in sedimentation of organic materials in the St. Lawrence Island Polynya region, Bering Sea. Mar Ecol Prog Ser 226:13-26

Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC (2007) Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002-2003. Deep-Sea Res II 54:2906-2918

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic–pelagic coupling in the western Arctic: role of cross-shelf advective processes. Deep-Sea Res II 52:3462-3477

Fay FH, Hills S, Quakenbush LT (1989) Determination of the age of walruses taken in the Alaskan subsistence catch, 1985-1987, together with the analysis of reproductive organs and stomach contents from the 1985 sample. U.S. Fish and Wildlife Service, Report 70181-13097-87, Anchorage, AK

Fay FH, Stoker SW (1982a) Analysis of reproductive organs and stomach contents from walruses taken in the Alaskan native harvest, spring 1980. U.S. Fish and Wildlife Service, Report 14-16-007-81-5216, Anchorage, AK

Fay FH, Stoker SW (1982b) Reproductive success and feeding habits of walruses taken in the 1982 spring harvest, with comparisons from previous years. Eskimo Walrus Commission, Final Report, Nome, AK

Feder HM, Day RH**,** Jewett SC, McCumby K, McGee S, Schonberg SV (1985) Infauna of the northeastern Bering and southeastern Chukchi Sea. In: Outer continental shelf environmental assessment program. U.S. Dept of Commerce, NOAA, Final Reports of Principal Investigators 32, Washington DC, pp 1-120

Feder H, Haflinger K, Hoberg M, McDonald J (1980) The infaunal invertebrates of the southeastern Bering Sea. IMS, Report R78-6, University of Alaska Fairbanks, AK

Fetzer I, Arntz WE (2008) Reproductive strategies of benthic invertebrates in the Kara Sea (Russian Arctic): adaptation of reproduction modes to cold water. Mar Ecol Prog Ser 356:189-202

Fleming RH, Heggarty D (1966) Oceanography of the southeastern Chukchi Sea. In: Wilimovsky NJ (ed) Environment of the Cape Thompson Region, Alaska. USAEC, Oakridge, TN, pp 697-754

Folk RL, Ward WC (1957) Brazos River Bar - A study in the significance of grain size parameters. J Sediment Petrol 27:3-26

Grebmeier JM (1987) The ecology of benthic carbon cycling in the northern Bering and Chukchi Seas. PhD Thesis, University of Alaska Fairbanks, AK

Grebmeier JM (1992) Benthic processes on the shallow continental shelf. In: Nagel P (ed) Results of the third joint US-USSR Bering & Chukchi Sea expedition (BERPAC), summer 1988, U.S. Fish and Wildlife Service, Washington DC, pp 243-251

Grebmeier JM (1993) Studies on pelagic-benthic coupling extended onto the Russian continental shelf in the Bering and Chukchi Seas. Cont Shelf Res 13:653-668

Grebmeier JM, Cooper LW (1995) Influence of the St. Lawrence Island Polynya on the Bering Sea benthos. J Geophys Res 100:4439-4460

Grebmeier JM, Cooper LW (2004) Biological implications of Arctic change, Oral Session 2: Paper 2. In: The ACIA international symposium on climate change in the Arctic: extended abstracts. AMAP Report 2004:4, Reykjavik, Iceland, pp 1-4

Grebmeier JM, Dunton KH (2000) Benthic processes in the northern Bering/Chukchi Seas: status and global change. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Marine Mammal Commission Workshop, Girdwood, AK, pp 80-93

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt L (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Grebmeier JM, Smith WO, Conover RJ (1995) Biological processes on Arctic continental shelves, ice-ocean-biotic interactions. In: Smith WO, Grebmeier JM (eds) Arctic oceanography: marginal ice zones and continental shelves: Coastal Estuarine Stud 49:231-261

Grey M, Boulding EG, Brookfield ME (2005) Shape differences among boreholes drilled by three species of naticid gastropods. J Mollus Stud 71:253-256

Hart MW, Palmer AR (1987) Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. J Exp Mar Biol Ecol 197:101-120

Holthe T (1986) Evolution, systematics and distribution of the Polychaeta Terebellomorpha, with a catalogue of the taxa and a bibliography. Gunneria 55:1-236

Hunt Jr. GL, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res II 49:5821-5853

Huston MA (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86:393-401

Johnson MD, Sherry TW (2001) Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. J Anim Ecol 70:546-560

Kirkegaard JB (1992) Havbørsteorme. I. Errantia. Danmarks Fauna 83:1-416

Kirkegaard JB (1996) Bathyl and abyssal polychaetes (sedentary species). Galathea Reports 17:57-77

Komar PD, Allan J, Dias-Mendez GM, Marra JJ, Ruggiero P (2000) El Niño and La Niña: erosion processes and impacts, Vol1, Paper 2. In: Abstracts of the 27th international conference on coastal engineering. Sydney, Australia, pp 2414-2427

Lovvorn JR, Richman SE, Grebmeier JM (2003) Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. Polar Biol 26:259-267

Maslanik JA, Serreze MC, Barry RG (1996) Recent decreases in Arctic summer ice cover and linkages to atmospheric circulation anomalies. Geophys Res Lett 23:1677-1680

Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997) Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proc Natl Acad Sci USA 94:14530-14535

Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Can J Zool 81:734-742

Moore SE, Stafford KM, Mellinger DK, Hildebrandet JA (2006) Listening for large whales in the offshore waters of Alaska. Bioscience 56:49-55

Morton B, Peharda M, Harper EM (2007) Drilling and chipping patterns of bivalve prey predation by *Hexaplex trunculus* (Mollusca: Gastropoda: Muricidae). J Mar Biol Assoc UK 87:933-940

Naidu AS, Mowatt TC (1983) Sources and dispersal patterns of clay minerals in surface sediments from the continental-shelf areas off Alaska. Geol Soc Am Bull 94:841-854

Napp JM, Kendall Jr. AW, Schumacher JD (2000) A synthesis of biological and physical processes affecting the feeding environment of larval walleye Pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fish Oceanogr 9:147-162

Nihoul J, Adam P, Brasseur P, Deleersnijder E, Djenidi S, Haus J (1993). Three-dimensional general circulation model of the northern Bering Sea's summer ecohydrodynamics. Cont Shelf Res 13:509-542

Oro D, Furness RW (2002) Influences of food availability and predation on survival of kittiwakes. Ecology 83:2516-2528

Overland JE, Roach AT (1987) Northward flow in the Bering and Chukchi Seas. J Geophys Res 92:7097-7105

Parkinson CL (2000) Variability of Arctic sea ice: the view from space, an 18-year record. Arctic 53:341-358

Parkinson CL, Cavalieri DJ (2002) A 21 year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. Ann Glaciol 34:441-446

Roach AT, Aagaard K, Pease CH, Salo SA, Weingartner T, Pavlov V, Kulakov M (1995) Direct measurements of transport and water properties through Bering Strait. J Geophys Res 100:18443-18457

Schumacher JD, Stabeno PJ (1998) Continental shelf of the Bering Sea. In: Robinson AR, Brink KH (eds) The sea, Vol XI. The global coastal ocean: regional studies and synthesis. John Wiley Inc., NY, pp 789-822

Serreze MC, Barrett A, Lo F (2005) Northern high latitude precipitation as depicted by atmospheric reanalyses and satellite retrievals. Mon Wea Rev 113:3407-3430

Serreze, MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533-1536

Sirenko BI, Koltun VM (1992) Characteristics of benthic biocenoses of the Chukchi and Bering Seas. In: Nagel P (ed) Results of the third joint US-USSR Bering and Chukchi Seas expedition (BERPAC), summer 1988. U.S. Fish and Wildlife Service, Washington DC, pp 251-261

Stabeno PJ, Reed RK (1994) Circulation in the Bering Sea basin by satellite tracked drifters. J Phys Oceanogr 24:848-854

Stabeno PJ, Schumacher JD, Ohtani K (1999) The physical oceanography of the Bering Sea. In: Loughlin TR, Ohtani K (eds) Dynamics of the Bering Sea. University of Alaska Sea Grant Press, Fairbanks, AK, pp 1-28

Stehn RA, Dau CP, Conant B, Butler Jr. WI (1993) Decline of spectacled eiders nesting in western Alaska. Arctic 46:264-277

Stoker S (1978) Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi Seas. PhD Thesis, University of Alaska Fairbanks, AK

Stoker S (1981) Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf. In: Hood DW, Calder JA (eds) The eastern Bering Sea shelf: oceanography and resources, Vol II, University of Washington Press, Seattle, pp 1069-1090

Takenouti AY, Ohtani K (1974) Currents and water masses in the Bering Sea: a review of Japanese work. In: Hood DW, Kelly EJ (eds) Oceanography of the Bering Sea with emphasis on renewable resources. University of Alaska at Fairbanks, AK, pp 39-57

Vinnikov KV, Robock A, Stouffer RJ, Walsh JE, Parkinson CL, Cavalieri DJ, Mitchell JFB, Garrett D, Zakharov VF (1999) Global warming and northern hemisphere ice

extent. Science 286:1934-1937

Woodgate RA, Aagaard K, Weingartner T (2006) Interannual changes in the Bering Strait fluxes of volume, heat and freshwater between 1991 and 2004. Geophys Res Lett Doi:10.1029/2006GL026931

Wyllie-Echeverria T, Wooster WS (1998) Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish Oceanogr 7:159-170

CHAPTER 2:

A comparison of Pacific walrus stomach contents between 2006 and the 1980s around St. Lawrence Island

2.1 ABSTRACT

Alterations in walrus behavior and foraging habitat (benthic communities), caused by climate change over the last 20+ years, may be correlated with reduced food for Pacific walruses (*Odobenus rosmarus divergens*). Since dietary changes can indicate altered food availability, this project compared stomach contents from walruses harvested near St. Lawrence Island in 2007 to those harvested in the 1980s. No significant differences were detected in counts, weights, frequencies, and species composition of prey items between time periods. A significantly lower proportion of walruses had food in their stomachs in 2007, perhaps because a larger proportion of 2007 samples were from fasting postpartum females. Although the non-significant results may be attributed to a small sample size in 2007, they suggest that a large change is unlikely to have occurred in the prey base. A dietary change, though, may not be evident if the Pacific walrus population has undergone a redistribution and/or decline.

2.2 INTRODUCTION

Pacific walruses (*Odobenus rosmarus divergens*) are an important species. Native communities along the Bering and Chukchi Sea coasts, such as those on St. Lawrence Island, have depended on walruses for food and raw materials for thousands of years (Langdon 1995, Garlich-Miller and Burn 1999). As benthic feeders, walruses also structure bottom communities through their foraging activities. Walruses excavate infaunal prey by moving their snouts and vibrissae and by sucking and expelling water,

leaving distinctive pits and furrows (Oliver et al. 1983, Oliver et al. 1985, Fukuyama and Oliver 1985, Ray et al. 2006). Through excavation, they displace, injure and kill "nonprey" infauna, create new habitat and space, attract scavenging species and re-suspend sediments (Oliver et al. 1983, Fukuyama and Oliver 1985, Oliver et al. 1985).

Over the last 20+ years, changes in the distributions of major bivalve species, declines in benthic biomass and abundance, declines in amphipod biomass, and increases in scyphomedusae have all been reported for the Bering Sea (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995, Brodeur et al. 1999, Grebmeier and Dunton 2000, Moore et al. 2003, Grebmeier and Cooper 2004, Dunton et al. 2005, Grebmeier et al. 2006, Coyle et al. 2007). These changes are thought to be due, in part, to alterations in sea ice characteristics, snow cover, and/or circulation patterns brought about by global warming (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995, Brodeur et al. 1999, Grebmeier and Dunton 2000, Moore et al. 2003, Derocher et al. 2004, Grebmeier and Cooper 2004, Dunton et al. 2005, Grebmeier et al. 2006) while other factors such as top-down control are discussed (Coyle et al. 2007).

Sea ice extent and thickness of both annual and multiyear sea ice has declined over the last twenty years (Maslanik et al. 1996, Vinnikov et al. 1999, Parkinson 2000, Comiso 2002, Parkinson and Cavalieri 2002, Comiso 2003, Serreze et al. 2005, Serreze et al. 2007). Walruses depend on ice as a substrate to haul out, rest, mate, and bear and nurse young (Fay 1974). Walruses also rely on ice floes for transport to new feeding areas (Fay 1974). During winter, both walrus sexes inhabit the central Bering Sea

temporary ice pack. Females and calves summer along the permanent ice pack edge of the Chukchi Sea during May-October while males summer along the southeastern and western Bering Sea (Fay 1982). Calves are born on the moving ice, mainly in May during the northward migration to the Chukchi Sea (Fay 1982).

While the present population size and health of Pacific walrus is unknown, prey quality or quantity may be changing through walrus behavior and environmental changes brought about by reduced summer sea ice (Pungowiyi 2000, Marz 2006, Metcalf and Robards 2008). In the past, females and young have inhabited ice year-round (Fay 1982). With decreases in summertime extent of ice, there may be increased competition among walruses near remaining ice for food resources (Pungowiyi 2000, Marz 2006). Walruses may also haul out more often and for longer periods on land as summer ice disappears, resulting in local benthic communities being heavily exploited and forcing walruses to travel farther offshore to feed (Pungowiyi 2000, Marz 2006). Walruses may be further limited in foraging when sea ice retreats beyond the continental shelf (Metcalf and Robards 2008). Walruses have been seen diving and presumably foraging at a depth of approximately 100 meters and are unlikely to be able to forage beyond the shelf break (Fay and Burns 1988).

Walruses may be especially vulnerable to changes in food supply because they are selective feeders (Fay 1982, Laidre et al. 2008, Metcalf and Robards 2008). In the Bering and Chukchi Seas, walruses preferentially feed on bivalves and gastropods although they also can consume cnidarians, nemerteans, priapulid worms, scyphozoans, anthozoans, hydrozoans, polychaetes, sipunculids, echiurans, cephalopods, brachiopods,

bryozoans, thoracicans, mysids, cumaceans, amphipods, isopods, decapods, holothurians, echinoids, ophiuroids, ascidians, urochordates, and vertebrates (Fay et al. 1977, Fay 1982, Fay and Stoker 1982a, Fay and Stoker 1982b, Fay et al. 1984, Fay et al. 1989, Sheffield 1997, Dehn et al. 2007).

If walrus food supply has changed over the past 20^{+} years, this may be reflected in a dietary change. For instance, a hypothesis of food limitation might be supported if unit prey size decreased while the frequency of energetically costly prey, such as echnioderms, increased (Sheffield 1997). Many dietary studies of ice associated pinnipeds have examined stomach contents (Frost and Lowry 1980, Lowry et al. 1980a, Lowry et al. 1980b, Bradstreet and Finley 1983, Finley and Evans 1983, Smith 1987, Dehn et al. 2007). Prey items are primarily identified from hard parts although some soft parts are identifiable (Sheffield 1997, Sheffield et al. 2001).

This study evaluated whether walrus diet, as evidenced by stomach contents, significantly changed between 2007 and the 1980s near St. Lawrence Island. The hypotheses tested included were that between 2007 and the 1980s: (1) the frequency of occurrence of prey items in walrus stomachs collected near St. Lawrence Island was not significantly different, (2) prey item counts in walrus stomachs collected near St. Lawrence Island were not significantly different, and (3) prey item weights in walrus stomachs collected from St. Lawrence Island were not significantly different.

2.3 METHODS

A total of 34 walruses were harvested in May 2007 by hunters from the villages of Savoonga (n = 20) and Gambell (n = 14) on St. Lawrence Island (Figure 2.1). For

every animal, hunters provided date and location of kill, and gender. Reproductive information also was recorded for females, such as milk and fetus presence, and a reproductive tract description. This information was recorded as part of a larger, bio-monitoring project with the Eskimo Walrus Commission and U.S. Fish and Wildlife Service assessing multiple parameters of the Pacific walrus population.

If food was present in a stomach, a one-gallon sub-sample of the contents was collected after total volume was visually estimated. Each sub-sample was taken from the anterior end of the stomach where prey are least digested. Contents were placed in one gallon jars, labeled, and frozen within 24 hours. If the jar could not be filled completely with stomach contents from the anterior end, then all contents were collected. Each filled jar weighed approximately 2,268 g (5 lbs).

In the laboratory, samples were thawed and strained through separate 0.15 mm nylon paint-strainer bags. Stomach contents were then sieved through a 2 mm mesh sieve, preserved in 10% formalin, and transferred into 50% isopropanol. Prey items were identified and sorted into the lowest possible taxonomic level. Prey items were counted, blotted dry, and weighed to the nearest centigram. Any remaining unidentified fragments, digested material and sediment particles (predominately rocks) were weighed to the nearest centigram. Sediment was examined in this study because the amount of sediment in stomach samples may be proportional to the amount of foraging effort expended by walruses (Fay and Stoker 1982b). Shells are usually absent in walrus stomachs, so identification of bivalves was based on feet and siphons while gastropods were identified by operculae (Vibe 1950, Brooks 1954, Mansfield 1958, Fay et al. 1977, Fay 1982).

Operculae and other diagnostic hard parts can persist long after organisms die. With only hard remnants of a prey item, it is difficult to determine the number of individuals of that species consumed, establish recent consumption of the prey item, or to obtain weight values that reasonably reflect the original biomass of the prey (Sheffield 1997, Fay and Stoker 1982a). Therefore, hard fragments not attached to tissue were recorded as trace occurrence and not included in counts or weights following methods established by Fay and Stoker (1982a). Sediment particles that were too congealed and/or small to effectively separate from other material also were recorded as trace and not weighed.

Stomach content data from 2007 were compared to stomach content data from Savoonga and Gambell collected in 1980, 1982, and 1985 (Fay and Stoker 1982a, Fay and Stoker 1982b, Fay et al. 1989). Sampling protocols among years varied slightly. In 1980, sub-samples (volume unknown) of mixed stomach contents were collected, drained in paint-strainer bags and after "large" solid parts had been removed, remaining particulate material was sieved through 2 mm mesh (Fay and Stoker 1982a). Methods in 1982 followed those of 1980 except that 5 lb sub-samples (approximate) of stomach contents were collected from the anterior end of stomachs (Fay and Stoker 1982b). In 1985, approximately 3 to 3.5 lb sub-samples of stomach contents were collected but samples were not sieved after being drained in paint-strainer bags (Fay et al. 1989). In 2007, to insure consistency, all prey items were sorted after being sieved through 2 mm mesh. Since the majority of 2007 fragments/prey items were larger than 2 mm, differences were probably negligible between sorting "large" fragments/prey items prior

to, or after, sieving. Since variation occurred in stomach sample volumes in all years, and could not be differentiated among historic data, all data collected from 2007 samples, regardless of volume, were included in analyses.

To determine if data from Savoonga and Gambell in 2007 could be pooled (no significant differences existed between samples by location or gender), the frequency of occurrence of dominant prey items (the top three prey items most frequently present in samples) were compared by location and by gender using z-tests. Median numbers and weights of dominant prey items (the top three prey items having the largest counts or wet weights in samples) in 2007 samples were additionally compared by gender and by location using Wilcoxon Rank-Sum tests. For these prey items, median values were obtained from all stomach samples within a group being compared. To determine if differences existed in walrus stomach content between 2007 and each of the previous years, median numbers and weights of dominant prey items (the top three prey items having the largest counts or wet weights in samples) were compared using a Kruskal-Wallis test. Median numbers and weights of these prey items were also compared between 2007 and each year using pairwise Wilcoxon Rank-Sum tests with a Bonferroni correction. If ties were found (same values occurring more than once among observations), an exact Wilcoxon Rank-Sum test was used to calculate an exact p value. The power of non-parametric tests was not determined in this project because it required simulations. Mean wet weights (grams) and counts of individual prey items in stomach content samples were calculated for all years although means could not be compared through non-parametric tests.

In addition to non-parametric tests, differences in the frequency of occurrence of dominant prey items (the top three prey items most frequently present in samples) between 2007 and each year was evaluated using pairwise z-tests with a Bonferroni correction. Multivariate analysis was used to examine whether differences existed based on the presence/absence of prey items found in stomach contents using the statistical software package, *Primer-E v6*. Two-way crossed ANOSIMs (Analysis of similarity) and MDS (Multi-dimensional scaling) plots were used. Bivalves, gastropods, crustaceans, and polychaetes were analyzed at the class level to reduce biases from a small sample size in 2007 and from stomach contents being in different stages of digestion.

2.4 RESULTS

Of the 34 walruses harvested in 2007 from Gambell and Savoonga, seven had prey in their stomachs. Compared with stomach content data from 1980 (n = 75) and 1982 (n = 37), a significantly higher proportion of walruses had empty stomachs in 2007 than in each of these other years (Figure 2.2; $z = 7.94$, $p \leq 0.0001$; $z = 6.34$, $p \leq 0.0001$; respectively). A significantly higher proportion of lactating, recently postpartum females were sampled in 2007 compared to 1980 and 1982 (Figure 2.2; $z = -6.24$, $p \leq 0.0001$; $z = -4.86$, $p \leq 0.0001$; respectively). For the above analyses, 1985 stomach content data were excluded because reproductive status of females was not recorded for many walruses sampled that year.

In 2007, bivalves and gastropods were dominant prey items, especially *Serripes*, *Panomya*, *Polinices*, and *Buccinum* (Figure 2.3, Appendices 2.1 and 2.2). *Serripes* and

Polinices were present in 71% of stomach content samples collected in 2007 while *Buccinum* occurred in 43% (Appendix 2.2). Although *Panomya* did not have a high frequency of occurrence within 2007 walrus stomach samples (14%), this genus dominated in mean wet weight (167.0 ± 167.0 g) and in mean number (131.7 ± 131.7) among prey items (Appendices 2.1 and 2.2). Echiurid worms also were very common in stomach contents with remnants found in 43% of samples. Additionally, Scyphozoa, Actiniaria (Cnidaria); Rhynchocoela; *Priapulus* (Priapula); *Nephthys (*Polychaeta); *Neptunea* (Gastropoda); *Mya* (Bivalvia); *Balanus* (Thoracica); *Argis*, *Hyas*, Paguridae (Decapoda), and Ascidiacea (Urochordata) were present (Appendices 2.1 and 2.2).

Prey items found in stomachs collected in the 1980s, but not in 2007, were *Arenicola*, *Brada*, *Lumbrinereis*, Maldanidae, *Pectinaria* (Polychaeta); *Golfingia* (Sipuncula); *Epitoneum*, *Margarites*, *Natica*, *Onchidiopsis*, *Solariella* (Gastropoda); *Astarte*, *Clinocardium*, *Hiatella*, *Liocyma*, *Nucula*, *Spisula*, *Thyasira*, Tellinidae, *Yoldia* (Bivalvia); Octopoda; Bryozoa; *Ampelisca*, *Byblis*, *Hippomedon*, *Protomedia* (Amphipoda); *Chionoecetes*, Crangonidae, *Sabinea* (Decapoda); *Cucumaria*, *Psolus* and *Thyonidium* (Holothuroidea), and *Ammodytes* (Osteichthyes). Prey species present only in walrus stomachs collected in 1980, compared to all other years, were *Pectinaria* (Polychaeta); *Epitoneum* (Gastropoda); *Clinocardium*, *Thyasira* (Bivalvia); *Hippomedon*, *Protomedia* (Amphipoda), and *Thyonidium* (Holothuroidea). All taxonomic groups of prey items found in walrus stomachs in 1982 were present in other years. Maldanidae (Polychaeta); *Sabinea*, *Chionoecetes* (Decapoda), and *Psolus* (Holothuroidea) were only present in stomach contents collected in 1985. Prey items found in walrus stomachs in

the 1980s, but not in 2007, mainly consisted of bivalve and crustacean species (Appendices 2.2, 2.3 and 2.4).

Based on z-tests, bivalves, gastropods, and crustaceans were not significantly different in their frequency of occurrence among 2007 walrus stomach contents either by gender or location (Table 2.1). Wilcoxon Rank-Sum tests also revealed no significant differences in the median counts or weights of these prey items by gender or location (Table 2.2). The frequency of bivalve, gastropod, and crustacean occurrence in 2007 was not significantly different from 1980, 1982, or 1985 (Table 2.3, Appendix 2.2). Multivariate analyses confirmed that walrus diet composition was very similar to the 1980s. Small Global R values were found when stomach data were compared in two-way crossed ANOSIMs using year and either gender or location as factors (Table 4). Since R values were close to zero, similar diet composition is indicated by year, gender and location despite significant p values by year (Table 2.4). Similar diet composition by gender and location also was supported by MDS analyses since data did not separate by these groups when plotted across all years (Figures 2.4 and 2.5). However, diet composition did partially separate by year when data were examined across all gender groups in an MDS plot (Figure 2.5).

Based upon the Wilcoxon Rank-Sum tests, significant differences in median bivalve number and weight were found in 2007 when compared to 1982 and 1985 (median numbers ± standard errors (SE): 16 ± 193 (n = 7), 84 ± 135 (n = 21), and 90 ± 38 (n= 35) and median weights ± SE being 210 ± 222 g (n = 7), 1038 ± 82 g (n = 21) and 1088 ± 89 g (n = 35) in 2007, 1985, and 1982, respectively (Table 2.5)). However, the

median number and weight of bivalves were not significantly different among years using a Kruskal-Wallis test (Table 2.6). Although differences were not detected in median crustacean number and weight based upon Wilcoxon Rank-Sum tests (Table 2.5), significant differences were found when Kruskal-Wallis tests were used (Table 2.6). However, since pairwise comparisons can not be performed using a Kruskal-Wallis test, differences among years can not be determined in this test. Median crustacean number and weight (± SE) were 8 ± 10 and 4 ± 3 g, respectively, in 1985 (n = 21) and 0 ± 3 and 0 ± 1 g in 2007 (n = 7).

2.5 DISCUSSION

In this study, diet composition in walruses harvested near St. Lawrence Island (SLI) in the spring was not significantly different between 2007 and the 1980s (Appendices 2.2, 2.3, and 2.4). Large bivalves, such as *Serripes* and *Panomya*, gastropods, and echiurid worms were common prey items in 2007 and in the 1980s around St. Lawrence Island (Fay and Stoker 1982 a, b, Fay et al. 1989). Although the present size and health of the Pacific walrus population is unknown, reports of lower reproductive rates in harvested female walruses in the 1990s may indicate that the population has approached the carrying capacity of the environment (Garlich-Miller et al. 2006). Changes have also been observed in walrus migration patterns and in the demographic structure of walrus groups at terrestrial haul-outs in the Gulf of Anadyr in recent years (Smirnov et al. 2004, Metcalf and Robards 2008). Since bivalves are a primary prey item for walruses, a potential reduction in this food resource may result in a walrus population redistribution or decline instead of a dietary change.

Changes in the abundance and distributions of several bivalve species, such as *Macoma calcarea, Eunucula bellotii and Nuculana pernula,* have been observed in the Bering Sea since 1988 (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004). Specifically, declines in *Macoma calcarea* and *Eunucula bellotii* have been reported in the polynya (an area of open water) region south of SLI (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004). These changes have been theorized to be related to increased settling of fine-grained sediments south of St. Lawrence Island and decreased circulation around the Gulf of Anadyr Gyre (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004). The present status of large, deep-dwelling bivalves, such as *Serripes* and *Mya*, in the Bering Sea remains unknown since they often can not be collected through traditional benthic van Veen grab sampling (Fay et al. 1977). However, it is possible that the distributions of these bivalves also are changing or declining in the Bering Sea due to alterations in sediment and circulation patterns.

It is possible that significant differences in walrus diet composition were not detected between 2007 and the 1980s in this study because the sample size in 2007 was small (n = 7) although no power calculations were done. Interestingly, bearded seal diets may have changed over the last 20+ years in the Bering and Chukchi Seas (Lowry et al. 1980b, Antonelis et al. 1994, Dehn et al. 2007). High frequencies of cephalopods, echiurids and holothurians were reported in recent Chukchi Sea bearded seal diets. In

previous studies, these prey items were determined to be of minor importance in bearded seal diets in the Bering and Chukchi Seas (Lowry et al. 1980b, Antonelis et al. 1994, Dehn et al. 2007). Since walruses and bearded seals have similar diets (Lowry et al. 1980b), the changes in bearded seal diets may indicate that food resources for walruses also have changed. Additionally, several benthic-feeding birds and mammals in the Bering Sea have declined in numbers and/or shifted their foraging grounds farther north, such as spectacled eiders and gray whales (Stehn et al. 1993, Lovvorn et al. 2003, Moore et al. 2003, Moore et al. 2006).

Local food resources may become depleted for walruses if they are restricted to smaller geographic areas as a result of declining summer sea ice. For example, in August 2007, unprecedented numbers of walruses were observed hauling out along North Chukotka and Alaska coasts (Anatoly Kochnev, TINRO-Centre; Dr. Chad Jay, USGS, pers. comm.). In the Bering Sea, a population of 150,000 to 200,000 walruses was estimated to consume between 3.3 and 4.4 million tons of food a year (Fay et al. 1977). Therefore, more intensive feeding on local inshore benthic communities may result in increased foraging effort by females with young (Pungowiyi 2000, Marz 2006). Observations of walrus calves swimming in open water alone in 2004, presumed abandoned by their mothers as they searched for food, may suggest increased foraging effort (Cooper et al. 2006). Food availability may become more reduced for walruses in early winter, compared to other seasons, due to increased competition between males and females foraging for food resources in the same area (Dr. Chad Jay, USGS; Brad Benter, ADF&G, pers. comm.).

If the Pacific walrus population is presently at the carrying capacity of the environment, then the continued loss of summer sea ice would likely intensify predation by walruses on near shore populations of deep-dwelling bivalves, such as *Serripes* and *Mya* (Dr. Ken Coyle, pers. comm.). If over-exploited, populations of these deep-dwelling bivalves may take a long time to recover since they are slow-growing (Ray et al. 2006). Bivalve population recovery may be prolonged further because of intermittent benthic recruitment (Ray et al. 2006). In the Bering Sea, benthic recruitment is strongly influenced by the timing of spring primary production and sea temperature (Sambrotto et al. 1986, Stabeno et al. 1998, Eslinger and Iverson 2001, Stabeno et al. 2001). During years in which ice retreat takes place late in April or May, early ice-associated blooms can occur beginning in mid-March. Early blooms are associated with cold water temperatures (< 2° C), which inhibit zooplankton grazing, enabling much of the phytoplankton production to reach the bottom and support benthic food webs (Napp et al. 2000, Hunt et al. 2002). In years in which water temperatures are relatively warm (> 4° C), the spring bloom occurs in late May or June and much of the primary production is cropped by zooplankton. The greater production of zooplankton would support pelagic communities (Hunt et al. 2002).

Based upon Wilcoxon Rank-Sum tests, significant differences in median bivalve number and weight within stomach contents were found in 2007 when compared to 1982 and 1985. However, these differences were not confirmed by any other statistical analyses. Although useful for comparison to results obtained through parametric tests, results of the Kruskal-Wallis and Wilcoxon Rank-Sum tests need to be interpreted

cautiously since they rely on count and weight values, which can be influenced by different digestion states and sample size variation.

Interpreting stomach content results can be complicated by biases associated with digestion (Sheffield 1997, Sheffield et al. 2001). Walrus prey are digested at different rates due to size differences and the amount of digestive-resistant tissues they contain (Sheffield et al. 2001). Therefore, prey that is easily digested, such as polychaetes, may be underestimated in dietary studies (Sheffield et al. 2001). Energy needs also vary between sexes and with reproductive status (Fay 1982, Gehnrich 1984, Sheffield 1997).

Despite significant p values when examining stomach data by year through ANOSIMs, Global R values were close to zero, indicating these differences were not large. R values are more reliable than p values because they measure differences between two or more groups in the dimensional space of the data whereas p values can be influenced by sample size (Clarke and Gorley 2006). Caution also must be used in interpreting the higher proportion of empty stomachs observed among sampled walruses in 2007 compared to the 1980s. Although a higher proportion of empty stomachs could suggest food limitation (Fay and Stoker 1982b), a large percentage of lactating females with newborns were present in the 2007 sample. Recently postpartum females are thought not to feed, or to eat very little, for some time (several weeks) after giving birth (Fay 1982). This behavior is attributed to the amount of time females spend tending their calves (Fay 1982, Gehnrich 1984). It is therefore likely that the higher proportion of empty stomachs in 2007 compared to the 1980s was a result of the higher proportion of postpartum females sampled in 2007. Females with young calves are preferred by

hunters in Savoonga and Gambell for their superior meat, ivory, and hides. Calf meat also is preferred and their hides are valued for making rawhide ropes (Sease 1986). Calves tend to stay with their mothers even after they are killed, making calves easily harvested (Burns 1965). Additionally, females with young are accessible to St. Lawrence Island communities because of their proximity to the spring migratory routes of parturient females (Fay 1955, Burns 1965, Garlich-Miller et al. 2006).

In summary, the findings of this study do not support a significant change in Pacific walrus diet composition between 2007 and the 1980s. However, it is important that studies continue that examine diet and body condition in Pacific walruses since changes have occurred in their behavior and in the environment, which could decrease food availability (Anatoly Kochnev, TINRO-Centre; Dr. Chad Jay, USGS, pers. comm.). Since declines and distributional shifts of several major bivalve species have been observed in the Bering Sea (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004), it is possible that deeper-dwelling bivalves, the primary prey of walruses, also have been reduced since the 1980s through either bottom-up or top-down processes. If a reduction has occurred in a primary food resource, the Pacific walrus population may have undergone a subsequent redistribution and/or decline instead of a dietary change.

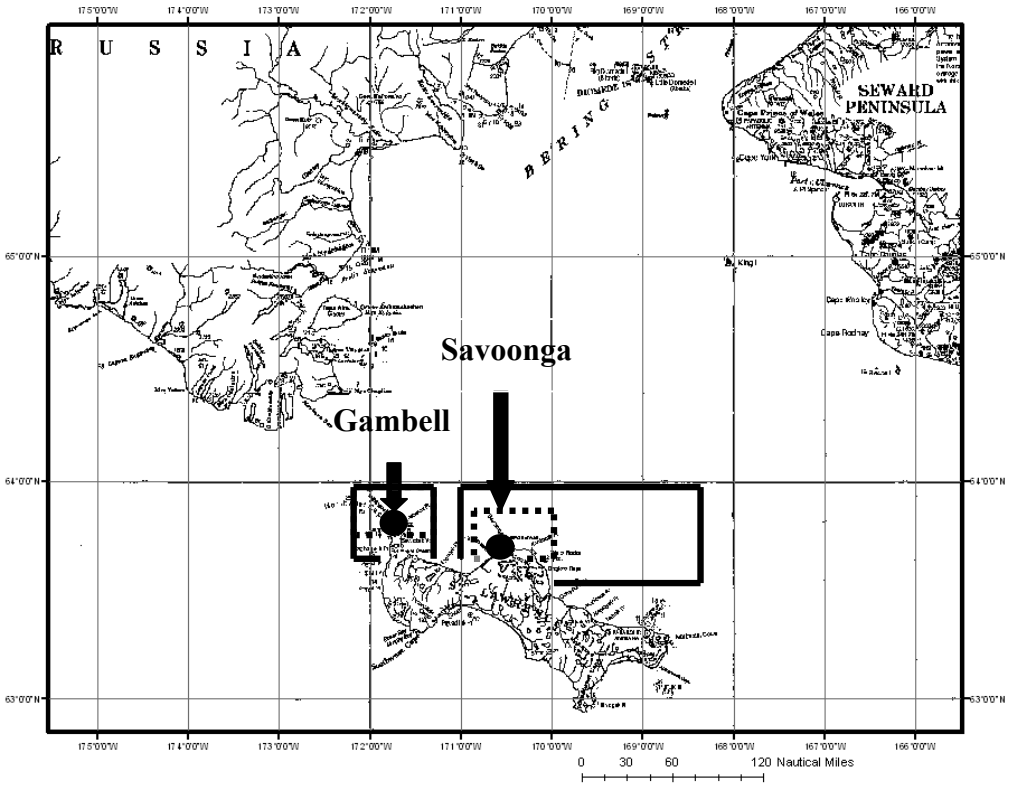

Figure 2.1. Map of St. Lawrence Island, Alaska, and the area of the Bering Sea in which walruses were harvested by subsistence hunters in 2007. Historical hunting grounds are represented by the dashed lines while 2007 hunting grounds are outlined by solid lines (Fay et al. 1977).

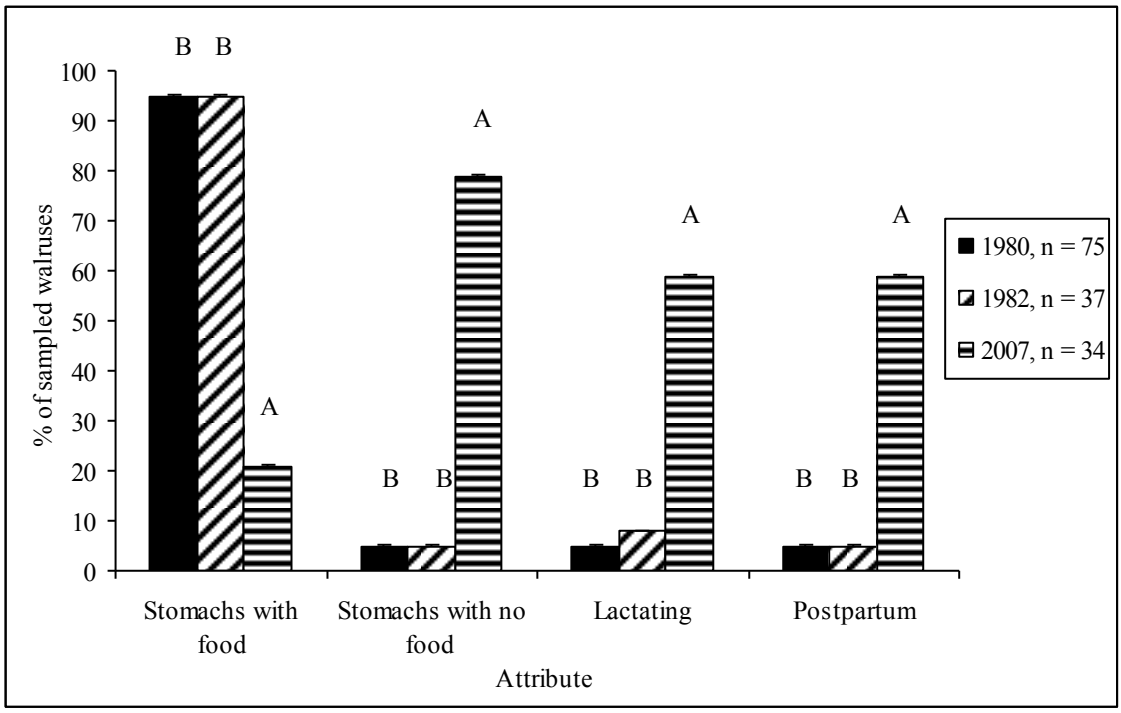

Figure 2.2. Percentage of sampled walruses, by year, with certain attributes ± standard errors (SE). SE = $\sqrt{(p\ (1-p)/\ n)}$ where p = percentage and n = number of samples. For each attribute, no significant differences exist between bars with identical letters as determined by a z-test with a Bonferroni correction. A = $p \leq 0.0001$ (significant p values < 0.025). Data from 1985 were excluded since descriptive information was not recorded for many of the sampled walruses.

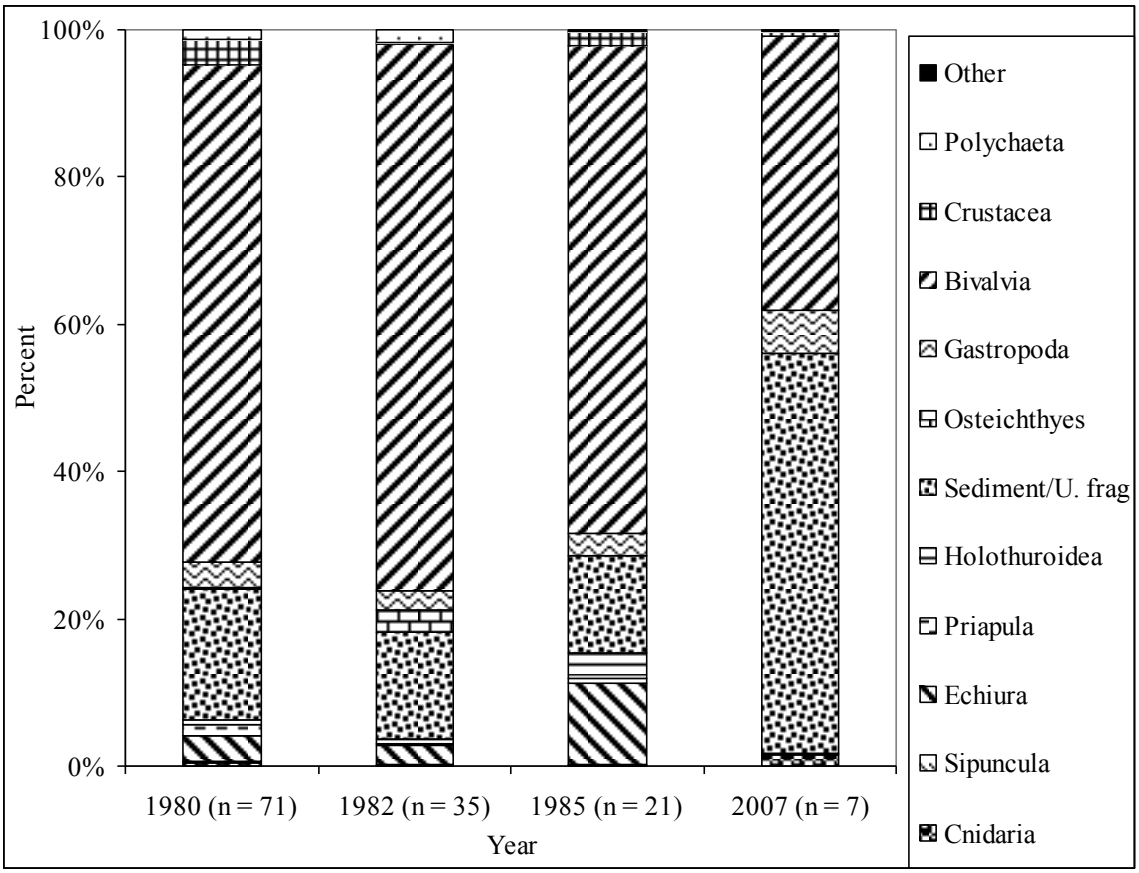

Figure 2.3. Percent contribution of prey items based upon weight (grams) in walrus stomachs by year. U. frag = unidentified fragments and "Other" = prey items composing less than 4% of total wet weight in samples.

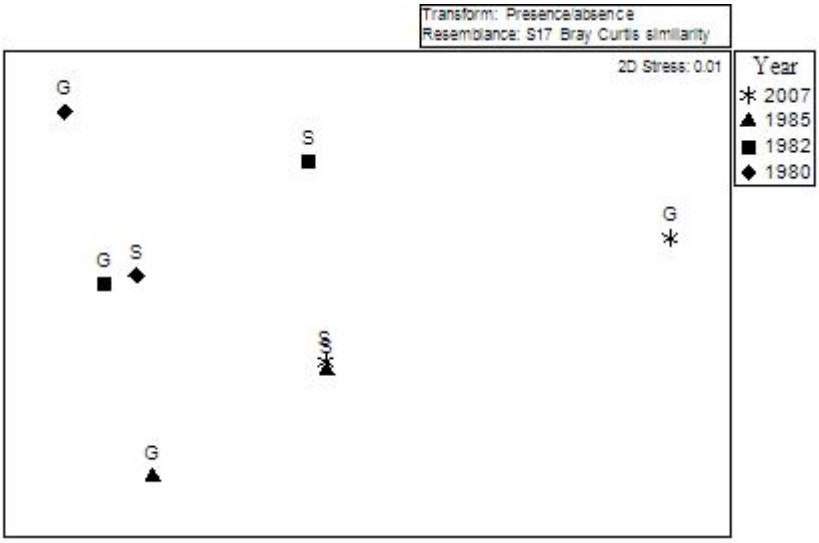

Figure 2.4. MDS plot comparing the presence/absence of prey items found in stomachs of walruses harvested near St. Lawrence Island by year and by location (S = Savoonga, G = Gambell).

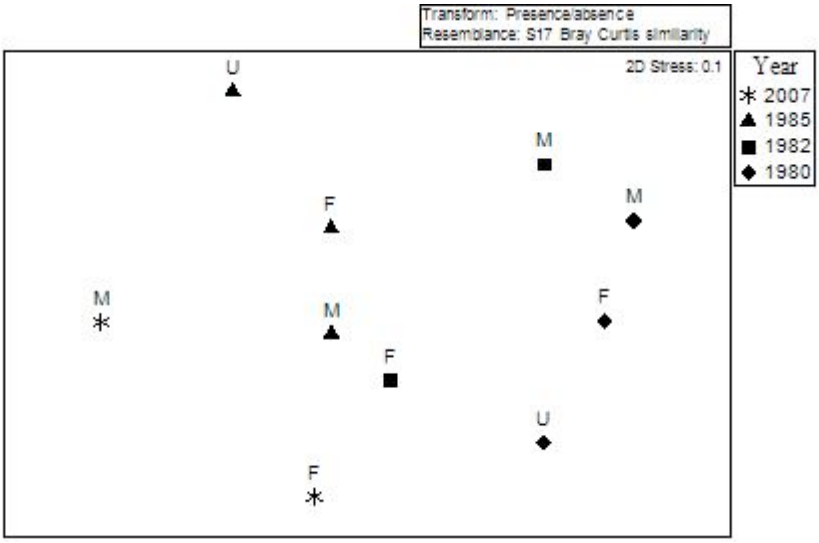

Figure 2.5. MDS plot comparing the presence/absence of prey items found in stomachs of walruses harvested near St. Lawrence Island by year and by gender (F = female, M = male, U = unknown).

Table 2.1. Z-test comparisons of the frequency of occurrence of prey items in 2007 walrus stomachs by location and by gender. Significant p values < 0.05.

	% Bivalves	% Gastropods	% Crustaceans
LOCATION: Savoonga n = 5 Gambell n = 2	Proportions exactly the same	z = 1.71 p = 0.0877	z = 0.794 p = 0.4274
GENDER: Females n = 4 Males n = 3	Proportions exactly the same	z = -0.935 p = 0.3496	z = 0.242 p = 0.8092

Table 2.2. Wilcoxon Rank-Sum tests comparing median weights and numbers of prey items in 2007 walrus stomachs by location and by gender. Significant p values < 0.05. Italicized p values determined by an exact Wilcoxon Rank-Sum test due to ties.

	Bivalves		Gastropods		Crustaceans	
	Wt	No	Wt	No	Wt	No
LOCATION: Savoonga n = 5 Gambell n = 2	W = 5 p = 1.000	W = 5 p = 1.000	W = 5.5 p = *0.8450*	W = 5.5 p = *0.8437*	W = 3.5 p = *0.5215*	W = 3.5 p = *0.5215*
GENDER: Females n = 4 Males n = 3	W = 5 p = 0.8571	W = 5 p = 0.8571	W = 6 p = *1.000*	W = 6 p = *1.000*	W = 10.5 p = *0.0792*	W = 10.5 p = *0.0792*

Table 2.3. Z-test comparisons (with Bonferroni correction) of the frequency of occurrence of prey items in 2007 walrus stomachs (n = 7) to walrus stomachs collected in 1980 (n = 71), 1982 (n = 35), and 1985 (n = 21). * = Significant p values < 0.02.

Year	% Bivalves	% Gastropods	% Crustaceans
1985	Proportions exactly the same	z = 0.00 p = 1.000	z = -0.455 p = 0.6488
1982	Proportions exactly The same	z = 0.00 p = 1.000	z = -1.83 p = 0.0676
1980	z = -0.450 p = 0.6528	z = 0.686 p = 0.4926	z = -0.132 p = 0.8949

Table 2.4. Two-way crossed ANOSIM comparisons of presence/absence of prey items in walrus stomachs across years (1980, 1982, 1985, 2007), gender and location (Savoonga and Gambell). * = Significant p values < 0.05.

	Global R value	P value	n
Differences between years (across all location groups)	0.184	0.001*	8
Differences between years (across all gender groups)	0.181	0.001*	10
Differences between locations (across all year groups)	0.053	0.162	8
Differences between gender (across all year groups)	0.019	0.330	10

Table 2.5. Wilcoxon Rank-Sum tests (with Bonferroni correction) comparing median numbers and weights of prey items in 2007 stomach contents (n = 7) to walrus stomachs collected in 1980 (n = 71), 1982 (n = 35), and 1985 (n = 21). * = Significant p values < 0.02. Italicized p values determined by an exact Wilcoxon Rank-Sum test due to ties.

	Bivalves		Gastropods		Crustaceans	
Year	Wt	No	Wt	No	Wt	No
1985	W = 28 p = *0.0158**	W = 24 p = 0.0070*	W = 74 p = *0.9788*	W = 85 p = *0.5390*	W = 48 p = *0.1587*	W = 46 p = *0.1284*
1982	W = 52 p = 0.0157*	W = 49 p = *0.0131**	W = 131 p = *0.7736*	W = 110.5 p = *0.6839*	W = 138 p = *0.5328*	W = 138 p = *0.5326*
1980	W = 157 p = 0.1116	W = 144 p = 0.0690	W = 252 p = 0.958	W = 201.5 p = 0.4146	W = 181 p = 0.2319	W = 184.5 p = 0.2551

Table 2.6. Kruskal-Wallis tests of median numbers and weights of prey items found in walrus stomachs across years (1980, 1982, 1985, and 2007). H = Kruskal-Wallis statistic (discrepancy between rank sums). * = Significant p values < 0.05.

	Bivalves		Gastropods		Crustaceans	
	Wt	No	Wt	No	Wt	No
n	4	4	4	4	4	4
H	6.11	6.11	0.200	1.38	14.4	14.0
df	3	3	3	3	3	3
p value	= 0.1064	= 0.1063	= 0.9775	= 0.7093	= 0.0024*	= 0.0029*

2.6 LITERATURE CITED

Antonelis GA, Melin SR, Bukhtiyarov YA (1994) Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. Arctic 47:74-79

Bradstreet MSW, Finley KJ (1983) Diet of ringed seals (*Phoca hispida*) in the Canadian high Arctic. LGL Limited, Toronto, Ontario

Brodeur RD, Mills CE, Overland JE, Walters GE, Schumacher JD (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish Oceanogr 8:296-306

Brooks JW (1954) A contribution to the life history and ecology of the Pacific walrus. Alaska Cooperative Wildlife Research Unit, Special Report 1, University of Alaska Fairbanks, AK

Burns JJ (1965) The walrus in Alaska: its ecology and management. Alaska Department of Fish and Game, Juneau, AK

Clarke KR, Gorley RN (2006) Primer-E v6: User manual/tutorial. PRIMER-E Ltd, Plymouth, UK

Comiso JC (2002) Correlation and trend studies of the sea-ice cover and surface temperatures in the Arctic. Ann Glaciol 34:420-428

Comiso JC (2003) Warming trends in the Arctic from clear-sky satellite observations. J Clim 16:3498-3510

Cooper LW, Ashjian CJ, Smith SL, Codispoti LA, Grebmeier JM, Campbell RG, Sherr EB (2006) Rapid seasonal sea-ice retreat in the Arctic could be affecting Pacific walrus (*Odobenus rosmarus divergens*) recruitment. Aquat Mam 32:98-102

Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC (2007) Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002-2003. Deep-Sea Res II 54:2906-2918

Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167-181

Derocher AE, Lunn NJ, Stirling I (2004) Polar bears in a warming climate. Integr Comp Biol 44:163-176

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic–pelagic coupling in the western Arctic: role of cross-shelf advective processes. Deep-Sea Res II 52:3462–3477

Eslinger DL, Iverson RL (2001) The effects of convective and wind-driven mixing on spring phytoplankton dynamics in the southeastern Bering Sea middle shelf domain. Cont Shelf Res 21:627-650

Fay FH (1955) The Pacific walrus (*Odobenus rosmarus divergens*): spatial ecology, life history, and population. PhD Thesis, University of British Columbia, BC

Fay FH (1974) The role of ice in the ecology of marine mammals of the Bering Sea. In: Hood DW, Kelley EJ (eds) Oceanography of the Bering Sea. IMS, University of Alaska Fairbanks, AK, pp 383-399

Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. N Am Fauna 74:1-279

Fay FH, Bukhtiyarov YA, Stoker SW, Shults LM (1984) Foods of the Pacific walrus in winter and spring in the Bering Sea. In: Soviet-American cooperative. Research on marine mammals, Pinnipeds, Vol 1. U.S. Department of Commerce, NOAA, NMFS, pp 81-88

Fay FH, Burns JJ (1988) Maximal feeding depth of walruses. Arctic 41:239-240

Fay FH, Feder HM, Stoker SW (1977) An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. National Technical Information Service, Report PB-273-505, Springfield, VA

Fay FH, Hills S, Quakenbush LT (1989) Determination of the age of walruses taken in the Alaskan subsistence catch, 1985-1987, together with the analysis of reproductive organs and stomach contents from the 1985 sample. U.S. Fish and Wildlife Service, Report 70181-13097-87, Anchorage, AK

Fay FH, Stoker SW (1982a) Analysis of reproductive organs and stomach contents from walruses taken in the Alaskan Native harvest, spring 1980. U.S. Fish and Wildlife Service, Report 14-16-007-81-5216, Anchorage, AK

Fay FH, Stoker SW (1982b) Reproductive success and feeding habits of walruses taken in the 1982 spring harvest, with comparisons from previous years. Eskimo Walrus Commission, Final Report, Nome, AK

Finley KJ, Evans CR (1983) Summer diet of the bearded seal (*Erignathus barbatus*) in the Canadian high Arctic. Arctic 36:82-89

Frost KJ, Lowry LF (1980) Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can J Zool 58:1601-1607

Fukuyama AK, Oliver JS (1985) Sea star and walrus predation on bivalves in Norton Sound, Bering Sea, Alaska. Ophelia 24:17-36

Garlich-Miller JL, Burn DM (1999) Estimating the harvest of Pacific walrus, *Odobenus rosmarus divergens*, in Alaska. Fish Bull 97:1043-1046

Garlich-Miller JL, Quakenbush LT, Bromaghin JF (2006) Trends in age structure and productivity of Pacific walruses harvested in the Bering Strait region of Alaska, 1952-2002. Mar Mamm Sci 22:880-896

Gehnrich PH (1984) Nutritional and behavioral aspects of reproduction in walruses. MSc Thesis, University of Alaska Fairbanks, AK

Grebmeier JM (1992) Benthic processes on the shallow continental shelf. In: Nagel P (ed) Results of the third joint US-USSR Bering & Chukchi Sea expedition (BERPAC), summer 1988, U.S. Fish and Wildlife Service, Washington DC, pp 243-251

Grebmeier JM (1993) Studies on pelagic-benthic coupling extended onto the Russian continental shelf in the Bering and Chukchi Seas. Cont Shelf Res 13:653-668

Grebmeier JM, Cooper LW (1995) Influence of the St. Lawrence Island Polynya on the Bering Sea benthos. J Geophys Res 100:4439-4460

Grebmeier JM, Cooper LW (2004) Biological implications of Arctic change, Oral Session 2: Paper 2. In: The ACIA international symposium on climate change in the Arctic: extended abstracts. AMAP Report 2004:4, Reykjavik, Iceland, pp 1-4

Grebmeier JM, Dunton KH (2000) Benthic processes in the northern Bering/Chukchi Seas: Status and global change. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Marine Mammal Commission Workshop, Girdwood, AK, pp 80-93

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt L (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Hunt Jr. GL, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res II 49:5821-5853

Laidre KL, Stirling I, Lowry LF, Wiig O, Heide-Jorgensen MP and Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl 18 (Supplement):S97-S1125

Langdon SJ (1995) Increments, ranges, and thresholds: human population responses to climate change in northern Alaska. In: Peterson DL, Johnson DR (eds) Human ecology and climate change: people and resources in the far north. Taylor & Francis, Washington DC, pp 139-152

Lovvorn JR, Richman SE, Grebmeier JM (2003) Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. Polar Biol 26:259-267

Lowry LF, Frost KJ, Burns JJ (1980a) Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. Can J Fish Aquat Sci 37:2254-2261

Lowry LF, Frost KJ, Burns JJ (1980b) Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33:330-342

Mansfield AW (1958) The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus), in the eastern Canadian Arctic. J Fish Res Board Can 653:1-146

Marz S (2006) Ice-dependent marine mammals in Alaska: a survey of background information and issues of concern regarding: ice seals, Pacific walrus, polar bears and bowhead whales. Alaska Oceans Program Report, Anchorage, AK

Maslanik JA, Serreze MC, Barry RG (1996) Recent decreases in Arctic summer ice cover and linkages to atmospheric circulation anomalies. Geophys Res Lett 23:1677-1680

Metcalf V, Robards M (2008) Sustaining a healthy human-walrus relationship in a dynamic environment: challenges for comanagement. Ecol Appl 18 (Supplement):S148 - S156

Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Can J Zool 81:734-742

Moore SE, Stafford KM, Mellinger DK, Hildebrandet JA (2006) Listening for large whales in the offshore waters of Alaska. Bioscience 56:49-55

Napp JM, Kendall Jr. AW, Schumacher JD (2000) A synthesis of biological and physical processes affecting the feeding environment of larval walleye Pollock (*Theragra chalcogramma*) in the eastern Bering Sea. Fish Oceanogr 9:147-162

Oliver JS, Kvitek RG, Slattery PN (1985) Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. J Exp Mar Biol Ecol 91:233-246

Oliver JS, Slattery PN, O'Connor EF, Lowry LF (1983) Walrus, *Odobenus rosmarus*, feeding in the Bering Sea: a benthic perspective. Fish Bull 81:501-512

Parkinson CL (2000) Variability of Arctic sea ice: the view from space, an 18-year record. Arctic 53:341-358

Parkinson CL, Cavalieri DJ (2002) A 21 year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. Ann Glaciol 34:441-446

Pungowiyi C (2000) Native observations of change in the marine environment of the Bering Strait region. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Marine Mammal Commission Workshop, Girdwood, AK, pp 26-29

Ray GC, McCormick-Ray J, Berg P, Epstein HE (2006) Pacific walrus: benthic bioturbator of Beringia. J Exp Mar Biol Ecol 330:403-419

Sambrotto RN, Niebauer HJ, Goering JJ, Iverson RL (1986) Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Cont Shelf Res 5:161-198

Sheffield G (1997) Walrus feeding: a re-examination. MSc Thesis, University of Alaska Fairbanks, AK

Sheffield G, Fay FH, Feder H, Kelly BP (2001) Laboratory digestion of prey and interpretation of walrus stomach contents. Mar Mamm Sci 17:310-330

Sease JL (1986) Historical status and population dynamics of the Pacific walrus. MSc Thesis, University of Alaska Fairbanks, AK

Serreze MC, Barrett A, Lo F (2005) Northern high latitude precipitation as depicted by atmospheric reanalyses and satellite retrievals. Mon Wea Rev 113:3407-3430

Serreze, MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533-1536

Sirenko BI, Koltun VM (1992) Characteristics of benthic biocenoses of the Chukchi and Bering Seas. In: Nagel P (ed) Results of the third joint US-USSR Bering and Chukchi Seas expedition (BERPAC), summer 1988. U.S. Fish and Wildlife Service, Washington DC, pp 251-261

Smirnov G, Litovka M, Pereverzev A, Tneskin V, Klimenko Y, Rultyntegreu N (2004) Conservation and environmental monitoring of coastal walrus haul-outs in the Gulf of Anadyr in 2003. National Fish and Wildlife Foundation, Technical Report, Washington DC

Smith TG (1987) The ringed seal, *Phoca hispida*, of the Canadian western Arctic. Can Bull Fish Aquat Sci 216:1-81

Stabeno PJ, Bond NA, Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the southeastern Bering Sea. Fish Oceanogr 10:81-98

Stabeno PJ, Schumacher JD, Davis RF, Napp JM (1998) Under-ice observations of water column temperature, salinity, and spring phytoplankton dynamics: eastern Bering Sea shelf. J Mar Res 56:239-255

Stehn RA, Dau CP, Conant B, Butler Jr. WI (1993) Decline of spectacled eiders nesting in western Alaska. Arctic 46:264-277

Vibe C (1950) The marine mammals and the marine fauna in the Thule district (northwest Greenland) with observations on ice conditions in 1939-41. Meddelelser om Grønland 150:1-115

Vinnikov KV, Robock A, Stouffer RJ, Walsh JE, Parkinson CL, Cavalieri DJ, Mitchell JFB, Garrett D, Zakharov VF (1999) Global warming and northern hemisphere ice extent. Science 286:1934-1937

GENERAL CONCLUSIONS

In this study, results suggested significant increases occurred in benthic invertebrate biomass and abundance (mainly due to the family Nuculidae) within a specific study area within the St. Lawrence Island Polynya (SLIP) between 1970-1974 and 2006. This contrasts other benthic studies that have reported declines in benthic invertebrate biomass and abundance, e.g., declines in amphipod biomass, and declines in several bivalve species such as *Eunucula bellotii* and *Macoma calcarea* in the SLIP and in the Chirikov Basin north of St. Lawrence Island over the last 20+ years (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier 1993, Grebmeier and Cooper 1995, Grebmeier et al. 1995, Grebmeier and Dunton 2000, Moore et al. 2003, Grebmeier and Cooper 2004, Dunton et al. 2005, Grebmeier et al. 2006, Coyle et al. 2007).

Benthic communities within and north of the SLIP may have significantly changed over the last 20+ years due to either bottom-up or top-down processes. Examples of bottom-up processes that could influence benthic communities in the Bering Sea are changes in sediment, carbon, and nutrient supply rates to the benthos (Stoker 1978, Sambrotto et al. 1986, Grebmeier 1987, Sirenko and Koltun 1992, Stabeno et al. 1998, Eslinger and Iverson 2001, Stabeno et al. 2001). Previous findings (Grebmeier and Cooper 1995, Grebmeier and Dunton 2000) suggested increased settling of fine-grained sediments as a cause for faunal changes within the SLIP, a conclusion that was supported in this study by a significantly lower proportion of stations classified as silt in 1970-1974 compared to 1990 within this region. The distributions of many benthic invertebrates, especially bivalves, are influenced by sediment characteristics due to different

preferences in grain size and chemical composition (Stoker 1978, Sirenko and Koltun 1992). Alternatively, an example of a top-down process that may contribute to benthic community changes is increased foraging by benthic-feeding predators as they approach or exceed their carrying capacity (Grebmeier and Cooper 1995, Grebmeier et al. 2006).

Significantly higher invertebrate biomass and abundance at stations sampled in 2006 compared to stations sampled in 1970-1974 may not be representative of the entire SLIP but reflect patchiness and/or small spatial scale. Bering Sea benthic communities are patchily distributed due to substrate, larval dispersal and/or predation (Stoker 1978). Since a small geographic area and number of stations were sampled in this study, the higher biomass and abundance observed at stations sampled in 2006 may be only locally applicable. However, it is possible that bivalves are more patchily distributed than previously thought within the SLIP and local changes in these distributions may have been obscured by the heterogeneity of large, post 1980 studies (Grebmeier 1992, Sirenko and Koltun 1992, Grebmeier and Cooper 1995, Grebmeier and Dunton 2000, Grebmeier and Cooper 2004). High spatial variability within 2006 stations could also have influenced results.

Despite the significant differences observed in SLIP benthic infaunal community structure in this study, no significant differences were found in stomach contents of walruses taken in subsistence hunts from St. Lawrence Island villages between the 1980s and 2007. Walruses prefer to prey on deep-dwelling bivalves, such as *Mya* and *Serripes*, which are difficult to sample through traditional benthic sampling methods (Fay et al. 1977). The status of deep-dwelling bivalves in the SLIP is presently unknown. The lack

of detectable change in diet, lack of understanding of the status of deep-dwelling bivalves, and the lack of reliable estimates of the Pacific walrus population size and distribution make it impossible to distinguish among alternative explanations. It is possible that changes have occurred in the status of the primary food source (bivalves) of walruses either through top-down (if walruses exceeded their carrying capacity) or through bottom-up processes. In such instances, a shift in diet would not necessarily be evident if the walrus population underwent a redistribution or decline (Lowry et al. 1980). Alternatively, the small sample size in this study may account for why a major difference in diet was not detected among walruses within the SLIP. Although no significant differences in walrus diet composition between the 1980s and 2007 were found in this study, other bottom-feeding predators in the Bering Sea have undergone dietary changes and/or population redistributions that some investigators attribute to changing foraging habitat. For example, there was a dramatic increase in documented gray whale mortalities and emaciated conditions linked to decreased benthic productivity in the Chirikov Basin in 2000 (LeBoeuf et al. 2000). Gray whales also have shifted their foraging grounds farther north into Bering Strait and extended their residence times in Arctic waters (Moore et al. 2006). Increases in the frequencies of cephalopods, echiurids and holothurians have been observed in bearded seal diets from the Bering and Chukchi Seas over the last 20+ years (Lowry et al. 1980, Antonelis et al. 1994, Dehn et al. 2007). Spectacled eiders in the SLIP appear to have shifted from primarily eating the bivalve species *Macoma calcarea* to *Nuculana pernula*; reflecting changed abundances since 1988 (Lovvorn et al. 2003). The number of spectacled eiders along the Yukon-

Kuskokwim Delta in western Alaska also has declined (Stehn et al. 1993). Regardless of the reason and contrary to this study's findings, these observations strongly suggest that food availability has become reduced for bottom-feeding predators in the Bering Sea.

Variability and changes in SLIP benthic communities will likely have different consequences for species within, and at, different trophic levels (Laidre et al. 2008). Predators that can feed in different geographic areas or switch between feeding on pelagic and benthic prey, like bearded seals, may be less affected by alterations in benthic community structure (Bluhm and Gradinger 2008). Predators with flexibility in their foraging behavior, diving physiology, enzymatic and/or functional morphology are more likely able to shift prey items or realms (Bluhm and Gradinger 2008). It is important to continue monitoring diet and body condition in walruses since they may be especially vulnerable to changes in benthic community structure (Bluhm and Gradinger 2008, Laidre et al. 2008, Metcalf and Robards 2008).

LITERATURE CITED

Antonelis GA, Melin SR, Bukhtiyarov YA (1994) Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the central Bering Sea, 1981. Arctic 47:74-79

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18 (Supplement):S148-S156

Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC (2007) Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002-2003. Deep-Sea Res II 54:2906-2918

Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167-181

Dunton KH, Goodall JL, Schonberg SV, Grebmeier JM, Maidment DR (2005) Multi-decadal synthesis of benthic–pelagic coupling in the western Arctic: role of cross-shelf advective processes. Deep-Sea Res II 52:3462-3477

Eslinger DL, Iverson RL (2001) The effects of convective and wind-driven mixing on spring phytoplankton dynamics in the southeastern Bering Sea middle shelf domain. Cont Shelf Res 21:627-650

Fay FH, Feder HM, Stoker SW (1977) An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. National Technical Information Service, Report PB-273-505, Springfield, VA

Grebmeier JM (1987) The ecology of benthic carbon cycling in the northern Bering and Chukchi Seas. PhD Thesis, University of Alaska Fairbanks, AK

Grebmeier JM (1992) Benthic processes on the shallow continental shelf. In: Nagel P (ed) Results of the third joint US-USSR Bering & Chukchi sea expedition (BERPAC), summer 1988, U.S. Fish and Wildlife Service, Washington DC, pp 243-251

Grebmeier JM (1993) Studies on pelagic-benthic coupling extended onto the Russian continental shelf in the Bering and Chukchi Seas. Cont Shelf Res 13:653-668

Grebmeier JM, Cooper LW (1995) Influence of the St. Lawrence Island Polynya on the Bering Sea benthos. J Geophys Res 100:4439-4460

Grebmeier JM, Cooper LW (2004) Biological implications of Arctic change, Oral Session 2: Paper 2. In: The ACIA international symposium on climate change in the Arctic: extended abstracts. AMAP Report 2004:4, Reykjavik, Iceland, pp 1-4

Grebmeier JM, Dunton KH (2000) Benthic processes in the northern Bering/Chukchi Seas: Status and global change. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Marine Mammal Commission Workshop, Girdwood, AK, pp 80-93

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt L (2006) A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464

Grebmeier JM, Smith WO, Conover RJ (1995) Biological processes on Arctic continental shelves, ice-ocean-biotic interactions. In: Smith WO, Grebmeier JM (eds) Arctic oceanography: marginal ice zones and continental shelves: Coastal Estuarine Stud 49:231-261

Laidre KL, Stirling I, Lowry LF, Wiig O, Heide-Jorgensen MP and Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. Ecol Appl 18 (Supplement):S97-S1125

LeBoeuf BJ, Perez-Cortes MH, Urban RJ, Mate BR, Ollervides UF (2000). High gray whale mortality and low recruitment in 1999: potential causes and implications. J Cetacean Res Manag 2:85-99

Lovvorn JR, Richman SE, Grebmeier JM (2003) Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. Polar Biol 26:259-267

Lowry LF, Frost KJ, Burns JJ (1980) Feeding of bearded seals in the Bering and Chukchi Seas and trophic interaction with Pacific walruses. Arctic 33:330-342

Metcalf V, Robards M (2008) Sustaining a healthy human-walrus relationship in a dynamic environment: challenges for comanagement. Ecol Appl 18 (Supplement):S148-S156

Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Can J Zool 81:734-742

Moore SE, Stafford KM, Mellinger DK, Hildebrandet JA (2006) Listening for large whales in the offshore waters of Alaska. Bioscience 56:49-55

Sambrotto RN, Niebauer HJ, Goering JJ, Iverson RL (1986) Relationships among vertical mixing, nitrate uptake and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Cont Shelf Res 5:161-198

Sirenko BI, Koltun VM (1992) Characteristics of benthic biocenoses of the Chukchi and Bering Seas. In: Nagel P (ed) Results of the third joint US-USSR Bering and Chukchi Seas expedition (BERPAC), summer 1988. U.S. Fish and Wildlife Service, Washington DC, pp 251-261

Stabeno PJ, Schumacher JD, Davis RF, Napp JM (1998) Under-ice observations of water column temperature, salinity, and spring phytoplankton dynamics: eastern Bering Sea shelf. J Mar Res 56:239-255

Stabeno PJ, Bond NA, Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the southeastern Bering Sea. Fish Oceanogr 10:81-98

Stehn RA, Dau CP, Conant B, Butler Jr. WI (1993) Decline of spectacled eiders nesting in western Alaska. Arctic 46:264-277

Stoker S (1978) Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. PhD Thesis, University of Alaska Fairbanks, AK

Appendix 1.1 Station number, date of sampling, water depth (m), latitude and longitude, and modal phi size of stations in which sediment and/or benthic composition was compared between years (1970-1974 (n = 38), 1984 (n = 1), 1990 (n = 23), 2006 (n = 7)).

Station Number	Date	Water depth (m)	Latitude °N	Longitude °W	Modal Phi Size
43	04/06/71	75	61.18	-173.79	3.25
44	07/08/74	56	61.37	-171.88	7
45	04/02/74	53	61.67	-171.17	4.5
46	04/02/74	48	61.76	-169.73	4.25
50	07/31/73	25	62.13	-167.88	3.5
51	04/01/71	25	62.15	-168.13	3.5
52	03/31/71	34	62.10	-168.38	3.5
53	07/08/74	48	62.08	-171.33	3.5
54	04/03/71	56	61.95	-171.75	3.5
57	03/01/72	86	61.37	-175.05	7
58	03/21/72	82	61.44	-174.45	3.5
59	03/20/72	78	61.43	-174.40	3.25
60	04/06/71	80	61.62	-174.40	3.5
61	03/01/72	66	61.73	-173.83	3.5
62	04/04/71	63	61.90	-173.42	3.5
63	03/02/72	55	61.93	-173.35	3.75
64	03/02/72	53	62.23	-172.65	3.5
66	02/12/70	70	62.45	-173.45	3.75
67	03/18/72	56	62.68	-172.60	4
68	03/03/72	48	62.65	-172.33	3.5
69	03/12/72	52	62.62	-172.10	2.75
70	02/13/70	54	62.58	-171.88	3.75
71	03/11/72	49	62.48	-172.17	3.25
72	07/08/74	38	62.51	-171.10	3
73	02/13/70	45	62.42	-170.00	2.75
75	03/31/71	23	62.60	-167.98	-0.31
76	07/31/73	31	62.59	-168.33	3
84	07/31/73	38	63.25	-168.45	2
85	07/31/73	16	63.25	-168.18	3
86	07/07/74	39	63.07	-168.32	3
87	07/07/74	32	62.86	-169.17	2.5
88	07/07/74	42	62.75	-170.05	3
89	07/08/74	43	62.90	-170.98	3
91	03/16/72	51	63.17	-171.55	2.75
92	03/05/72	55	62.95	-172.20	4
93	03/08/72	58	62.92	-172.18	4

Appendix 1.1 Cont'd. Station number, date of sampling, water depth (m), latitude and longitude, and modal phi size of stations in which sediment and/or benthic composition was compared between years (1970-1974 (n = 38), 1984 (n = 1), 1990 (n = 23), 2006 (n = 7)).

Station Number	Date (MM/DD/YY)	Water depth (m)	Latitude °N	Longitude °W	Modal Phi Size
94	03/06/72	54	62.98	-172.60	4
95	07/01/74	58	63.26	-172.05	3
148	07/09/84	55	63.10	-171.95	N/A
4	06/11/90	35	60.87	-169.00	4
6	06/12/90	40	61.70	-169.23	≥ 5
11	06/12/90	40	62.80	-169.50	3
12	06/12/90	29	62.67	-168.72	3
14	06/13/90	26	61.42	-167.83	4
20	06/13/90	18	62.62	-168.03	3
23/24	06/14/90	27	62.91	-168.98	3
25	06/14/90	25	63.03	-169.27	3
27	06/14/90	42	62.73	-170.22	3
28	06/14/90	36	62.46	-170.25	3
30	06/14/90	46	61.93	-170.37	≥ 5
32/33	06/15/90	49	61.13	-170.54	≥ 5
35	06/15/90	54	61.83	-171.76	≥ 5
40/41	06/16/90	43	62.87	-170.93	4
46	06/16/90	46	63.13	-171.35	3
47	06/16/90	50	62.97	-171.61	4
48/49	06/17/90	51	62.80	-171.90	4
51	06/17/90	56	62.33	-172.58	≥ 5
53/54	06/17/90	67	61.73	-173.47	≥ 5
55/56	06/18/90	78	62.02	-175.05	≥ 5
58	06/18/90	67	62.57	-173.83	≥ 5
60/61	06/18/90	65	62.98	-173.00	≥ 5
63/64	06/18/90	59	63.33	-172.26	≥ 5
1	03/23/06	57	61.75	-173.25	7.00
2	03/24/06	65	62.72	-173.73	7.00
3	03/25/06	65	62.83	-173.97	N/A
4	03/27/06	57	62.76	-172.68	7.00
5	03/28/06	42	62.77	-171.43	4.00
6	03/29/06	44	63.00	-171.78	3.00
7	03/30/06	50	63.04	-172.13	4.00

Appendix 1.2. Mean weight (grams/m^2) and mean abundance (indiv./m^2) ± 1 standard errors of stations sampled in 1970-1974 and 2006. For 1984 and 1990 stations, standard deviations were not available and so standard errors could not be calculated.

Station No.	Year	No. of replicates	Mean Weight Wt (grams/m^2)	Mean Abundance (indiv./m^2)
57	1970-1974	5	77.06 ± 17.27	116 ± 15
67	1970-1974	5	107.44 ± 21.08	764 ± 79
68	1970-1974	5	165.11 ± 36.20	468 ± 42
69	1970-1974	5	6.79 ± 2.41	156 ± 48
88	1970-1974	5	362.03 ± 65.74	1558 ± 251
89	1970-1974	5	245.14 ± 25.69	642 ± 55
92	1970-1974	5	290.77 ± 45.47	968 ± 75
93	1970-1974	5	139.78 ± 12.37	370 ± 38
94	1970-1974	5	137.06 ± 24.75	580 ± 68
148	1984	4	405.13	2293
27	1990	4	149.15	2713
40/41	1990	4	98.61	1538
47	1990	4	230.85	953
48/49	1990	4	316.99	1283
55/56	1990	4	1127.68	1603
58	1990	4	354.39	3360
60	1990	4	404.57	2253
1	2006	5	193.0 ± 49.21	874 ± 94
2	2006	4	960.46 ± 24.62	2583 ± 130
3	2006	5	570.34 ± 59.94	2050 ± 47
4	2006	5	376.72 ± 31.71	972 ± 72
5	2006	5	300.74 ± 59.16	1090 ± 98
6	2006	2	682.93 ± 89.55	2480 ± 110
7	2006	5	560.91 ± 86.27	1842 ± 227

Appendix 1.3. Families, or lowest taxonomic groups, present in sieve fractions (1 mm and 2.8 mm) among samples collected in 2006. Bold = taxonomic class. U = unidentified.

1 mm	2.8 mm
Ascidiacea	**Ascidiacea**
Bivalvia	**Bivalvia**
Cardiidae	Cardiidae
Lasaeidae	Lyonsiidae
Lyonsiidae	Mytilidae
Mytilidae	Nuculidae
Nuculidae	Nuculanidae
Nuculanidae	Tellinidae
Tellinidae	Thyasiridae
Thyasiridae	Veneridae
Veneridae	
Gastropoda	**Gastropoda**
Buccinidae	Cancellariidae
Cancellariidae	Cylichnidae
Cylichnidae	Naticidae
Conidae	U. Cephalaspidea
Littorinidae	
Naticidae	
Retusidae	
Trochidae	
U. Cephalaspidea	
Amphipoda	**Amphipoda**
Ampeliscidae	Ampeliscidae
Gammaridae	Gammaridae
Lysianassidae	Lysianassidae
Oedicerotidae	Oedicerotidae
Photidae	Pontoporeiidae
Phoxocephalidae	
Pontoporeiidae	
Pleustidae	
Stenothoidae	
Crangonidae	**Crangonidae**

Appendix 1.3 Cont'd. Families, or lowest taxonomic groups, present in sieve fractions (1 mm and 2.8 mm) among samples collected in 2006. Bold = taxonomic class. U = unidentified.

1 mm	2.8 mm
Cumacea	**Cumacea**
Diastylidae	Leuconidae
Leuconidae	
Isopoda	**Isopoda**
Idotheidae	Idotheidae
Polychaeta	**Polychaeta**
Ampharetidae	Ampharetidae
Amphictenidae	Amphictenidae
Arabellidae	Arabellidae
Capitellidae	Capitellidae
Cirratulidae	Cirratulidae
Lumbrineridae	Lumbrineridae
Maldanidae	Maldanidae
Nephtyidae	Nephtyidae
Onuphidae	Onuphidae
Orbiniidae	Orbiniidae
Flabelligeridae	Flabelligeridae
Glyceridae	Glyceridae
Phyllodocidae	Phyllodocidae
Polynoidae	Polynoidae
Scalibregmidae	Scalibregmidae
Sigalionidae	Sigalionidae
Sphaerodoridae	Spionidae
Spionidae	Sternaspidae
Sternaspidae	Terebellidae
Terebellidae	
Rhynchocoela	**Rhynchocoela**
Sipuncula	**Sipuncula**
Chiridotidae	**Chiridotidae**
Priapulidae	**Priapulidae**
Ophiuridae	**Ophiuridae**

Appendix 2.1. Wet weights (grams) and counts of prey items in 2007 walrus stomachs. Tr = only hard parts present or "trace occurrence" and U = unidentified.

ID Number	S07-0003		S07-0005		S07-0006		S07-0010	
Gender	♀		♂		♂		♀	
Location	Savoonga		Savoonga		Savoonga		Savoonga	
Taxa	Wt	No	Wt	No	Wt	No	Wt	No
Cnidaria								
U. Actiniaria	0	0	0	0	0	0	55.88	4
U. Scyphozoa	0	0	0	0	0	0	27.91	1
Rhynchocoela								
U. Rhynchocoela	0	0	0	0	0	0	2.32	1
Priapula								
Priapulus	0	0	0	0	0	0	3.11	4
Polychaeta								
Nephthys	0	0	0	0	0	0	4.81	2
Echiura								
Echiurus	0	0	Tr	Tr	Tr	Tr	Tr	Tr
Gastropoda								
Buccinum	0	0	Tr	Tr	0	0	Tr	Tr
Neptunea	Tr	Tr	0	0	0	0	74.53	9
Polinices	Tr	Tr	Tr	Tr	0	0	10.57	5
U. Gastropod	0	0	51.58	5	14.35	2	83.82	15
Bivalvia								
Mya	0	0	0	0	0	0	62.83	2
Serripes	0	0	76.17	15	493.60	43	99.84	9
U. Bivalve	167.30	16	174.66	16	116.15	13	47.30	2
Amphipoda								
Anoxyx	0.610	1	0	0	0	0	0	0
Decapoda								
Hyas	1.33	1	0	0	0	0	0	0
U. Paguridae	0	0	0	0	0	0	14.37	4
U. Decapod	0	0	Tr	Tr	0	0	0	0
U. Crustacean								
U. Crustacean	0	0	Tr	Tr	0	0	0	0
Other								
U. Fragments	53.78	0	171.80	0	47.92	0	86.84	0
Sediments	40.49	0	5.54	0	0.331	0	Tr	0

Appendix 2.1 Cont**.** Wet weights (grams) and counts of prey items in 2007 walrus stomachs. Tr = only hard parts present or "trace occurrence" and U = unidentified.

ID Number	S07-0011		G07-0079		G07-0136	
Gender	♂		♀		♀	
Location	Savoonga		Gambell		Gambell	
Taxa	Wt	No	Wt	No	Wt	No
Gastropoda						
Buccinum	0	0	0.682	1	0	0
Neptunea	2.53	1	47.94	11	0	0
Polinices	Tr	Tr	0.310	1	0	0
U. Gastropod	1.60	1	13.78	1	0	0
Bivalvia						
Panomya	0	0	0	0	1169.3	922
Serripes	9.43	3	0	0	40.68	1
U. Bivalve	30.04	9	37.47	4	478.99	447
Thoracica						
Balanus	0	0	0.443	1	0	0
Decapoda						
Argis	0	0	1.31	3	0	0
U. Paguridae	0	0	13.09	2	0	0
U. Crustacean						
U. Crustacean	Tr	Tr	Tr	Tr	0	0
Urochordata						
U. Ascidiacea	0	0	1.29	1	0	0
Other						
U. Fragments	73.69	0	30.40	0	137.16	0
Sediments	903.71	0	1191.62	0	107.78	0

Appendix 2.2. Percent frequency of occurrence of prey items in walrus stomachs by year. U = unidentified.

Taxa	2007 (n = 7) % Frequency of Occurrence	1985 (n = 21) % Frequency of Occurrence	1982 (n = 35) % Frequency of Occurrence	1980 (n = 71) % Frequency of Occurrence
Cnidaria				
U. Actiniaria	14	5	6	11
U. Scyphozoa	14	5	0	0
Rhynchocoela				
U. Rhynchocoela	14	0	3	0
Priapula				
Priapulus	14	38	31	65
Polychaeta				
Arenicola	0	5	17	3
Brada	0	0	3	6
Lumbrinereis	0	5	6	1
U. Maldanidae	0	10	0	0
Nephthys	14	24	29	15
Pectinaria	0	0	0	1
U. Polychaete	0	5	6	4
Sipuncula				
U. Sipunculid	0	10	0	0
Golfingia	0	0	11	17
Echiura				
Echiurus	43	62	26	39
Gastropoda				
U. Buccinidae	0	43	0	0
Buccinum	43	43	37	45
Epitoneum	0	0	0	3
Margarites	0	24	3	3
Neptunea	57	71	43	62
Natica	0	14	34	48
U. Naticidae	0	29	0	0
Onchidiopsis	0	29	0	3
Polinices	71	52	54	73
Solariella	0	0	0	4
U. Gastropod	71	14	54	62
Bivalvia				
Astarte	0	5	0	3

Appendix 2.2 Cont'd. Percent frequency of occurrence of prey items in walrus stomachs by year. U = unidentified.

Taxa	2007 (n = 7) % Frequency of Occurrence	1985 (n = 21) % Frequency of Occurrence	1982 (n = 35) % Frequency of Occurrence	1980 (n = 71) % Frequency of Occurrence
Bivalvia				
Clinocardium	0	0	0	3
Hiatella	0	10	0	11
Liocyma	0	0	0	3
Mya	14	100	83	90
Nucula	0	0	3	0
Panomya	14	90	0	0
Serripes	71	81	86	82
Spisula	0	0	31	3
Thyasira	0	0	0	1
U. Tellinidae	0	48	37	30
Yoldia	0	14	11	8
U. Bivalve	100	0	0	54
Cephalopoda				
U. Octopoda	0	0	6	1
Bryozoa				
U. Bryozoa	0	0	0	1
Thoracica				
Balanus	14	0	0	0
Amphipoda				
Ampelisca	0	10	3	0
Anoxyx	14	14	6	4
Byblis	0	0	3	0
Hippomedon	0	0	0	1
Protomedia	0	0	0	1
U. Amphipod	0	24	0	0
Decapoda				
Argis	14	24	20	3
Chionoecetes	0	52	0	0
Crangonidae	0	0	0	35
Hyas	14	19	17	44
U. Paguridae	29	33	20	14
Sabinea	0	5	0	0

Appendix 2.2 Cont'd. Percent frequency of occurrence of prey items in walrus stomachs by year. U = unidentified.

Taxa	2007 (n = 7) % Frequency of Occurrence	1985 (n = 21) % Frequency of Occurrence	1982 (n = 35) % Frequency of Occurrence	1980 (n = 71) % Frequency of Occurrence
U. Decapod	14	10	0	0
U. Crustacean				
U. Crustacean	43	10	0	3
Holothuroidea				
Cucumaria	0	67	14	1
Psolus	0	5	0	0
Thyonidium	0	0	0	32
Urochordata				
U. Ascidiacea	14	0	0	0
Pelonaia	0	0	3	7
U. Tunicate	0	0	0	4
Osteichthyes				
Ammodytes	0	0	26	3
U. Fishes	0	0	3	0
Other				
U. Shells	0	5	26	0
U. Fragments	100	100	77	39
Sediments	100	67	74	72

Appendix 2.3. Mean wet weights ± standard errors of prey items in walrus stomachs by year. Tr = only hard parts present or "trace occurrence" and U = unidentified.

Taxa	2007 (n = 7) Mean Wt (grams)	1985 (n = 21) Mean Wt (grams)	1982 (n = 35) Mean Wt (grams)	1980 (n = 71) Mean Wt (grams)
Cnidaria				
U. Actiniaria	8.0 ± 8.0	0.48 ± 0.48	2.51 ± 2.12	4.41 ± 2.05
U. Scyphozoa	4.0 ± 4.0	0.05 ± 0.05	0	0
Rhynchocoela				
U. Rhynchocoela	0.3 ± 0.3	0	0.03 ± 0.03	0
Priapula				
Priapulus	0.4 ± 0.4	8.21 ± 3.01	3.97 ± 1.52	17.41 ± 4.97
Polychaeta				
Arenicola	0	0.79 ± 0.79	14.29 ± 8.73	5.07 ± 3.57
Brada	0	0	0.03 ± 0.03	3.70 ± 2.70
Lumbrinereis	0	0.24 ± 0.24	0.09 ± 0.06	0.03 ± 0.03
U. Maldanidae	0	0.08 ± 0.06	0	0
Nephthys	0.7 ± 0.7	1.96 ± 1.53	7.80 ± 4.54	2.87 ± 1.61
Pectinaria	0	0	0	0.01 ± 0.01
U. Polychaete	0	0.19 ± 0.19	0.77 ± 0.69	2.55 ± 2.51
Sipuncula				
U. Sipunculid	0	3.00 ± 2.63	1.20 ± 0.66	0
Golfingia	0	0	0.83 ± 0.62	3.17 ± 1.55
Echiura				
Echiurus	Tr	162.38 ± 79.39	34.74 ±	41.75 ± 13.59
Gastropoda				
U. Buccinidae	0	13.02 ± 7.71	0	0
Buccinum	0.1 ± 0.1	0.92 ± 0.87	1.20 ± 0.66	2.52 ± 1.37
Epitoneum	0	0	0	Tr
Margarites	0	0.12 ± 0.07	Tr	0.01 ± 0.01
Neptunea	20.8 ± 12.3	20.37 ± 7.56	13.80 ± 6.88	16.53 ± 5.77
Natica	0	2.49 ± 1.81	1.71 ± 1.17	3.24 ± 1.31
U. Naticidae	0	3.25 ± 1.81	0	0
Onchidiopsis	0	0.64 ± 0.46	0	Tr
Polinices	2.7 ± 2.0	3.26 ± 2.13	2.94 ± 0.90	2.15 ± 0.38
Solariella	0	0	0	Tr
U. Gastropod	23.6 ± 12.1	2.70 ± 2.48	17.71 ± 8.29	16.35 ± 3.84
Bivalvia				
Astarte	0	0.01 ± 0.01	0	3.49 ± 3.49
Clinocardium	0	0	0	0.04 ± 0.03
Hiatella	0	58.48 ± 0.30	0	33.18 ± 16.73

Appendix 2.3 Cont'd. Mean wet weights ± standard errors of prey items in walrus stomachs by year. Tr = only hard parts present or "trace occurrence" and U = unidentified.

Taxa	2007 (n = 7) Mean Wt (grams)	1985 (n = 21) Mean Wt (grams)	1982 (n = 35) Mean Wt (grams)	1980 (n = 71) Mean Wt (grams)
Bivalvia				
Liocyma	0	0	0	0.14 ± 0.13
Mya	9.0 ± 9.0	269.57 ± 40.60	573.74 ± 100.31	544.67 ±
Nucula	0	0	0.03 ± 0.03	0
Panomya	167.0 ± 167.0	341.80 ± 72.07	0	0
Serripes	102.8 ± 66.8	296.64 ± 75.93	271.79 ± 54.47	208.46 ± 36.84
Spisula	0	0	55.94 ± 21.73	15.49 ± 13.67
Thyasira	0	0	0	0.01 ± 0.01
U. Tellinidae	0	5.70 ± 4.31	15.23 ± 10.13	4.27 ± 1.42
Yoldia	0	0.92 ± 0.70	0.80 ± 0.59	0.39 ± 0.19
U. Bivalve	150.3 ± 59.3	0	13.09 ± 0.00	53.29 ± 10.40
Cephalopoda				
U. Octopoda	0	0	0.29 ± 0.29	Tr
Bryozoa				
U. Bryozoa	0	0	0	0.03 ± 0.03
Thoracica				
Balanus	0.1 ± 0.1	0	0	0
Amphipoda				
Ampelisca	0	0.14 ± 0.14	0.03 ± 0.03	0
Anoxyx	0.1 ± 0.1	0.12 ± 0.10	0.07 ± 0.04	0.15 ± 0.10
Byblis	0	0	0.03 ± 0.03	0
Hippomedon	0	0	0	0.01 ± 0.01
Protomedia	0	0	0	0.01 ± 0.01
U. Amphipod	0	2.14 ± 1.85	0	0
Decapoda				
Argis	0.2 ± 0.2	4.64 ± 2.56	1.54 ± 1.26	18.27 ± 17.64
Chionoecetes	0	16.10 ± 6.78	0	0
Crangonidae	0	0	0	17.90 ± 8.23
Hyas	0.2 ± 0.2	0.43 ± 0.27	0.87 ± 0.43	4.87 ± 1.18
Paguridae	3.9 ± 2.5	1.05 ± 0.41	0.40 ± 0.21	0.58 ± 0.24

Appendix 2.3 Cont'd. Mean wet weights ± standard errors of prey items in walrus stomachs by year. Tr = only hard parts present or "trace occurrence" and U = unidentified.

Taxa	2007 (n = 7) Mean Wt (grams)	1985 (n = 21) Mean Wt (grams)	1982 (n = 35) Mean Wt (grams)	1980 (n = 71) Mean Wt (grams)
Decapoda				
Sabinea	0	Tr	0	0
U. Decapod	Tr	1.43 ± 1.33	0	0
U. Crustacean				
U. Crustacean	Tr	2.02 ± 1.97	0	0.46 ± 0.45
Holothuroidea				
Cucumaria	0	49.56 ± 19.16	9.37 ± 4.68	0.04 ± 0.04
Psolus	0	2.86 ± 2.86	0	0
Thyonidium	0	0	0	8.99 ± 2.98
Urochordata				
U. Ascidiacea	0.2 ± 0.2	0	0	0
Pelonaia	0	0	0.29 ± 0.29	0.25 ± 0.15
U. Tunicate	0	0	0	0.21 ± 0.13
Osteichthyes				
Ammodytes	0	0	31.49 ± 22.32	1.48 ± 1.41
U. Fishes	0	0	0.03 ± 0.03	0
Other				
U. Shells	0	0.24 ± 0.24	0.60 ± 0.58	0
U. Fragments	85.9 ± 19.3	133.12 ± 20.62	50.64 ± 9.07	37.62 ± 8.27
Sediments	374.9 ± 200.5	59.07 ± 26.59	145.58 ± 65.44	174.94 ±

Appendix 2.4. Mean counts ± standard errors of prey items in walrus stomachs by year. Tr = only hard parts present or "trace occurrence" and U = unidentified.

Taxa	2007 (n = 7) Mean No	1985 (n = 21) Mean No	1982 (n = 35) Mean No	1980 (n = 71) Mean No
Cnidaria				
U. Actiniaria	0.6 ± 0.6	0.05 ± 0.05	0.43 ± 0.40	0.76 ± 0.32
U. Scyphozoa	0.1 ± 0.1	0.01 ± 0.01	0	0
Rhynchocoela				
U. Rhynchocoela	0.1 ± 0.1	0	0.03 ± 0.03	0
Priapula				
Priapulus	0.6 ± 0.6	1.29 ± 0.53	0.69 ± 0.22	2.59 ± 0.56
Polychaeta				
Arenicola	0	0.08 ± 0.08	3.37 ± 2.28	0.63 ± 0.45
Brada	0	0	0.11 ± 0.11	9.00 ± 7.17
Lumbrinereis	0	0.14 ± 0.14	0.06 ± 0.04	0.03 ± 0.03
U. Maldanidae	0	0.06 ± 0.05	0	0
Nephthys	0.3 ± 0.3	0.62 ± 0.40	1.60 ± 0.77	0.35 ± 0.13
Pectinaria	0	0	0	0.01 ± 0.01
U. Polychaete	0	0.14 ± 0.14	0.80 ± 0.77	0.49 ± 0.43
Sipuncula				
U. Sipunculid	0	0.57 ± 0.48	Tr	0
Golfingia	0	0	0.20 ± 0.11	0.93 ± 0.40
Echiura				
Echiurus	Tr	27.71 ±16.23	8.23 ± 5.26	12.77 ± 4.17
Gastropoda				
U. Buccinidae	0	2.50 ± 1.02	0	0
Buccinum	0.2 ± 0.2	0.33 ± 0.29	0.29 ± 0.13	0.86 ± 0.54
Epitoneum	0	0	0	Tr
Margarites	0	0.17 ± 0.11	Tr	0.01 ± 0.01
Neptunea	3.5 ± 1.9	4.65 ± 1.55	1.97 ± 0.88	4.93 ± 2.08
Natica	0	0.90 ± 0.65	1.14 ± 0.78	1.85 ± 0.66
U. Naticidae	0	1.26 ± 0.75	0	0
Onchidiopsis	0	0.57 ± 0.23	0	Tr
Polinices	1.5 ± 0.9	1.35 ± 0.71	1.69 ± 0.49	1.25 ± 0.20
Solariella	0	0	0	Tr
U. Gastropod	3.4 ± 2.0	0.04 ± 0.04	4.29 ± 1.91	8.73 ± 2.34
Bivalvia				
Astarte	0	0.01 ± 0.01	0	16.30 ± 16.30
Clinocardium	0	0	0	0.04 ± 0.03
Hiatella	0	172.57 ± 136.48	0	60.39 ± 27.89

Appendix 2.4 Cont'd. Mean counts ± standard errors of prey items in walrus stomachs by year. Tr = only hard parts present or "trace occurrence" and U = unidentified.

Taxa	2007 (n = 7) Mean No	1985 (n = 21) Mean No	1982 (n = 35) Mean No	1980 (n = 71) Mean No
Bivalvia				
Liocyma	0	0	0	0.10 ± 0.09
Mya	0.3 ± 0.3	41.18 ± 8.00	77.29 ± 15.26	103.56 ± 19.70
Nucula	0	0	0.03 ± 0.03	0
Panomya	131.7 ± 131.7	21.04 ± 4.09	0	0
Serripes	10.1 ± 5.9	17.14 ± 3.32	17.46 ± 4.30	11.70 ± 1.88
Spisula	0	0	4.40 ± 1.84	4.94 ± 4.37
Thyasira	0	0	0	0.01 ± 0.01
U. Tellinidae	0	8.83 ± 6.63	49.74 ± 36.50	13.44 ± 5.27
Yoldia	0	1.19 ± 0.92	1.60 ± 1.17	0.96 ± 0.49
U. Bivalve	72.4 ± 62.5	0	Tr	Tr
Cephalopoda				
U. Octopoda	0	0	0.03 ± 0.03	Tr
Bryozoa				
U. Bryozoa	0	0	0	0.01 ± 0.01
Thoracica				
Balanus	0.1 ± 0.1	0	0	0
Amphiphoda				
Ampelisca	0	0.52 ± 0.52	0.06 ± 0.06	0
Anoxyx	0.1 ± 0.1	0.14 ± 0.10	0.06 ± 0.04	0.10 ± 0.06
Byblis	0	0	0.03 ± 0.03	0
Hippomedon	0	0	0	0.01 ± 0.01
Protomedia	0	0	0	0.01 ± 0.01
U. Amphipod	0	0.43 ± 0.29	0	0
Decapoda				
Argis	0.4 ± 0.4	1.57 ± 0.71	0.89 ± 0.45	4.42 ± 4.20
Chionoecetes	0	4.89 ± 1.47	0	0
U. Crangonidae	0	0	0	6.08 ± 2.94
Hyas	0.1 ± 0.1	0.29 ± 0.20	0.31 ± 0.16	2.29 ± 0.58
U. Paguridae	0.9 ± 0.6	1.11 ± 0.48	0.40 ± 0.22	0.46 ± 0.20
Sabinea	0	0.10 ± 0.10	0	0
U. Decapod	Tr	0.10 ± 0.10	0	0
U. Crustacean	Tr	0.11 ± 0.10	0	0.01 ± 0.01

Appendix 2.4 Cont'd. Mean counts ± standard errors of prey items in walrus stomachs by year. Tr = only hard parts present or "trace occurrence" and U = unidentified.

Taxa	2007 (n = 7) Mean No	1985 (n = 21) Mean No	1982 (n = 35) Mean No	1980 (n = 71) Mean No
Holothuroidea				
Cucumaria	0	2.81 ± 1.19	0.31 ± 0.15	0.01 ± 0.01
Psolus	0	0.19 ± 0.19	0	0
Thyonidium	0	0	0	0.65 ± 0.16
Urochordata				
U. Ascidiacea	0.1 ± 0.1	0	0	0
Pelonaia	0	0	0.11 ± 0.11	0.20 ± 0.10
U. Tunicate	0	0	0	0.06 ± 0.03
Osteichthyes				
Ammodytes	0	0	18.54 ± 11.10	2.27 ± 2.25
U. Fishes	0	0	0.03 ± 0.03	0
Other				
U. Shells	0	Tr	Tr	0
U. Fragments	Tr	Tr	Tr	Tr
Sediments	Tr	Tr	Tr	Tr